
MOLECULAR PHYLOGENETICS, CHARACTER EVOLUTION, AND SUPRAGENERIC CLASSIFICATION OF LAMIOIDEAE (LAMIACEAE)¹

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ABSTRACT

This paper presents a phylogenetic analysis of Lamiaceae subfam. Lamioideae (including subfamily Pogostemonoideae) based on sequences of the *trnL* intron, *trnL-trnF* intergenic spacer, and *rps16* intron of the plastid genome. It is the first analysis that includes all major lamioideid and pogostemonoid genera. Monophyly of Lamioideae s.l. (i.e., including Pogostemonoideae) is strongly supported, with *Cymaria* Benth. as its sister group, and Pogostemonoideae, which sometimes has been recognized as a subfamily, is subsumed in Lamioideae. On the basis of the phylogenetic hypothesis, Lamioideae is divided into nine tribes. Three new tribes are established: Gomphostemmatae Scheen & Lindqvist, Phlomisae Mathiesen, and Leucadeae Scheen & Ryding. The other six tribes are: Pogostemoneae Briq., Synandreae Raf., Stachydeae Dumort., Leonureae Dumort., Lamieae Coss. & Germ., and Marrubieae Vis. The genus *Betonica* L. is reestablished. The results also strongly suggest that the genera *Stachys* L., *Sideritis* L., *Ballota* L., and *Leucas* R. Br. are polyphyletic or paraphyletic. The results were used to examine evolution of non-molecular characters.

Key words: Character evolution, classification, Lamiaceae, Lamioideae, molecular phylogenetics, morphology, Pogostemonoideae.

During the past decade, the number of molecular phylogenetic studies on plants has increased at a rapid pace. Advances in comparative DNA sequencing and methods for phylogeny reconstruction have made it possible to investigate a broad range of systematic and evolutionary questions for large numbers of taxa. One important result of this has been that molecular phylogenetic studies have sometimes overturned relationships suggested from traditional classifications. One such example is the Lamiaceae, which is a large, cosmopolitan angiosperm family with 236 genera and more than 7000 species (Harley et al., 2004).

The Lamiaceae has traditionally been regarded as one of the most distinctive angiosperm families,

readily identified by a suite of morphological characters (Benthams, 1876; Briquet, 1895–1897). A close yet discrete relationship with Verbenaceae was also suggested by the early system builders. However, modern phylogenetic analyses of morphological data have suggested that Lamiaceae was polyphyletically derived within Verbenaceae (Abu-Asab & Cantino, 1992; Cantino, 1992a), with the consequence that some previously verbenaceous taxa were reassigned to Lamiaceae to preserve the family's monophyly (Cantino, 1992b; Cantino et al., 1992). These phylogenetic conclusions were later corroborated with comparative DNA sequence analysis (Wagstaff & Olmstead, 1997; Wagstaff et al., 1998). Currently, seven subfamilies are recognized within Lamiaceae

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(Harley et al., 2004), of which Nepetoideae is the largest, one of the most easily defined, and probably the best investigated.

Throughout the taxonomic history of Lamiaceae, the circumscription of another large subfamily, Lamioideae, has changed considerably (see, e.g., Cantino, 1992b). Recently, Cantino et al. (1992) considered the pogostemonoid labiates a separate subfamily, although they drew no clear distinction between Pogostemonoideae and Lamioideae. The pogostemonoid taxa were characterized by having stamens of equal length, and lamiod labiates by presence of laballic acid and an unusual embryo sac. However, stamen length is likely to be an evolutionarily labile character, and the potential value of the other two characters is limited by the small taxonomic sample in which they have been documented (e.g., Hagemann et al., 1967; Wunderlich, 1967; Cantino, 1992a, b, and references therein). On the other hand, pericarp structure (Ryding, 1995) and pollen morphology (Abu-Asab & Cantino, 1994) provide no distinction between the two groups. Moreover, phylogenetic segregation of the Pogostemonoideae and Lamioideae has been only poorly supported by chloroplast DNA (cpDNA) evidence, whereas the monophyletic group consisting of both subfamilies is strongly supported (Wagstaff et al., 1998). Consequently, in the latest classification of the Lamiaceae, pogostemonoid taxa have been subsumed into Lamioideae (Harley et al., 2004). However, the position of this subfamily within Lamiaceae is still uncertain, depending on a more conclusive circumscription of the lamiod labiates. Nevertheless, molecular phylogenetic results have suggested Scutellarioideae as the closest relatives of the Pogostemonoideae–Lamioideae clade (Wagstaff & Olmstead, 1997; Wagstaff et al., 1998).

So, given the changing delimitation of the subfamily, how can the Lamioideae be diagnosed as currently circumscribed? As is apparent from the conflicting traditional classifications, no one set of morphological characters seems to distinguish this group from other labiate groups. They are mostly non-aromatic herbs or shrubs (or rarely small trees) that otherwise have the typical labiate bauplan. The inflorescences are thyrsoïd or raceme-like, with single- to many-flowered cymes, and corollas that are zygomorphic and usually 2-lipped. They are distinguished from nepetoid labiates by having the pollen grains tricolpate and 2-celled when shed, seeds albuminous, and embryos spatulate (Cantino & Sanders, 1986). They differ from the remaining members of the family by having gynobasic styles. Within the subfamily, 63 genera including up to 1257 species are presently recognized (Harley et al., 2004). The taxonomic distribution of species within the subfamily is characterized by a large number of monotypic genera (approximately one

third), and ca. 50% of the total number of species belonging to only four genera—*Leucas* R. Br., *Phlomis* L., *Sideritis* L., and *Stachys* L. These numbers seem very unbalanced and may reflect the general deficiency of morphological synapomorphies and taxonomic challenges that this subfamily represents.

Although it has a cosmopolitan distribution, Lamioideae are rare outside of Eurasia and Africa. Only six genera and about 70 species are native to the New World. Lamioideae have many members in tropical regions of the world, particularly Africa and Southeast Asia. For example, pogostemonoids are largely tropical East Asian. Otherwise, Lamioideae are predominantly distributed in the Northern Hemisphere, and numerous genera are widespread in temperate to subtropical Eurasia; several are Asian endemics, whereas others are also widely spread throughout temperate Europe or are restricted to Europe and the Mediterranean region.

Although Lamioideae comprise the second largest subfamily in Lamiaceae, the subfamily has not previously been the subject of targeted phylogenetic research, and suprageneric relationships within the subfamily are poorly understood. Within the subfamily, only limited phylogenetic studies at infrageneric and/or intergeneric levels have been published (e.g., Ryding, 1998; Barber et al., 2002; Lindqvist & Albert, 2002; Scheen et al., 2008; Scheen & Albert, 2009).

Our principal purpose with the present study is to ascertain major generic groupings and phylogenetic relationships within the subfamily Lamioideae. We applied molecular phylogenetic data in order to assess several questions concerning morphological trends and taxonomic subdivisions, including a first attempt at constructing a strongly needed classification of the major suprageneric groupings discovered.

MATERIALS AND METHODS

TAXON AND OUTGROUP SELECTION

A representative sample of subfamilies Lamioideae and Pogostemonoideae was selected using 167 accessions representing 159 species (13% of all species) from 50 genera (80% generic representation). See Table 1 for details on voucher information, GenBank accession numbers, and references. All major genera of lamiod and pogostemonoid labiates were included. Only a few monotypic or small genera have been omitted because no material was available or because attempts to amplify DNA failed. To evaluate the monophyly of subfamilies Lamioideae and Pogostemonoideae, 28 species of other Lamiaceae were also included: two species from subfamily Ajugoideae, 14 species from subfamily Nepetoideae,

two species from subfamily Prostantheroideae, two species from subfamily Scutellarioideae, one species from subfamily Symphorematoideae, two species from subfamily Viticoideae, and five species that have not been ascribed to a subfamily (genera incertae sedis in Harley et al., 2004). Two species of Verbenaceae were selected as outgroup for all analyses. Most of the sequences for these 30 species were retrieved from GenBank (see Table 1).

DNA EXTRACTION, POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION, AND SEQUENCING

DNA was extracted from silica-dried leaves (vouchers held at O or BHO) or from leaf fragments taken from herbarium specimens held at A, C, GH, O, P, S, TEX, UPS, US, and WU. Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. Several DNA samples from a previous study were also used (Lindqvist & Albert, 2002). The *trnL* intron and *trnL-trnF* intergenic spacer were amplified using the universal primers of Taberlet et al. (1991), either as one fragment (hereafter referred to as the *trnL-F* region) using primers c and f or as two separate fragments using primers c and d, and e and f, respectively. The *rps16* intron was amplified using the primers *rpsF* and *rpsR2R* (Oxelman et al., 1997). When DNA of low quality was used as template, the following internal primers new to this study were used in addition to the two mentioned above: *rpsLR* (5'-TCATTGGGTTTACACATTACTTCG-3') and *rpsLF* (5'-CGGGAATCGACTGTCCATAG-3'). PCRs were performed in volumes of 25 μ L using the AmpliTaq DNA polymerase buffer II kit (Applied Biosystems, Foster City, California, U.S.A.) containing 0.2 mM of each dNTP, 0.04% bovine serum albumin (BSA), 0.01 mM tetramethylammonium chloride (TMACl), 0.8 μ M of each primer, and 2 μ L unquantified genomic DNA. Amplifications were performed in a GeneAmp PCR System 9700 (Applied Biosystems) using a program consisting of 4 min. at 94°C followed by 30 cycles of 30 sec. denaturation (94°C), 30 sec. annealing (60°C), and 1 min. extension (72°C), ending with a final 4 min. extension (72°C). Successful PCR reactions were purified using QIAquick PCR Purification Kit (Qiagen) or 8 μ L 10 $\times$ diluted exoSAP-IT (USB Corporation, Cleveland, Ohio, U.S.A.) per reaction. Cycle sequencing was performed using the same primers as in the PCR and the BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems). Quarter reactions were prepared, i.e., 2 μ L BigDye, 2 μ L 5 $\times$ buffer, 3 μ L cleaned PCR product, and distilled water to a volume of 10 μ L, and run using the program recommended by the manufacturer on GeneAmp PCR System 9700 (Applied

Biosystems). Sequenced products were either purified with CENTRI SEP Columns (Princeton Separations, Adelphia, New Jersey, U.S.A.) or precipitated in ethanol and sodium acetate to remove excess dye terminators before being analyzed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems). Most of the *rps16* intron sequences were processed at the CEES DNA Laboratory (University of Oslo). In addition, sequences from previous studies of lamioid labiates were used (Lindqvist & Albert, 2002; Scheen et al., 2008; Scheen & Albert, 2009; see Table 1).

ALIGNMENT AND PHYLOGENY RECONSTRUCTIONS

Sequences were assembled and edited using Sequencher 4.1.4 (Gene Codes, Ann Arbor, Michigan, U.S.A.) before being aligned manually using BioEdit (Hall, 1999). Most of the alignments were straightforward; ambiguities due to gaps were solved by following the advice of Kelchner (2000). Insertions/deletions (indels) were coded as present/absent (A/T) and added to the matrices as additional, unordered characters using the program SeqState (Müller, 2005) following the simple indel coding of Simmons and Ochoterena (2000).

Previous studies have shown that when analyzed separately, the *trnL-F* region and *rps16* intron produce compatible topologies (e.g., Wallander & Albert, 2000; Jobson et al., 2003; Paton et al., 2004). Therefore, the data sets resulting from the *trnL-F* region and *rps16* intron were concatenated a priori to parsimony analyses. Two resulting matrices were analyzed: (1) data without indel coding, i.e., indels treated as missing data, and (2) data with indels coded and added to the matrix as binary characters.

Parsimony analyses were run in TNT (Goloboff et al., 2003) with the new technology option in a driven search using sectorial searches, tree-drifting, and tree-fusing (Goloboff, 1999). Analyses were run until a stabilized consensus had occurred twice using equal character weights and tree bisection-reconnection (TBR) branch swapping. Additional TBR branch swapping was performed on trees resulting from the initial search to find additional equally parsimonious trees. Parsimony jackknifing and bootstrap support for internal branches was also estimated using TNT. One thousand replicates were conducted, each performing TBR branch swapping with 10 random entry orders and saving one tree per replicate. Absolute support values were reported. Because the bootstrap support values were comparable to the jackknife values, only the latter are reported here.

A cursory maximum likelihood (ML) analysis using the PHYML (Guindon & Gascuel, 2003) was performed using the online web server at <<http://www.atgc-montpellier.fr/phyml/>>. Specifications for

Table 1. List of species, voucher, and GenBank accession information for specimens used in the molecular phylogeny of subfamily Lamioideae.

Taxon	Origin/voucher information	GenBank accession no.		
		<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron
Lamioideae				
<i>Achyrosperrum africanum</i> Baker	Cameroon, <i>M. Etuge & D. W. Thomas 441</i> (UPS)	FJ854246	FJ854133	FJ853999
<i>A. carvalhoi</i> Gürke	Malawi, <i>I. Hedberg 89133</i> (UPS)	FJ854248	FJ854135	FJ854001
<i>A. cryptanthum</i> Baker	Malawi, <i>R. K. Brummitt 10762</i> (UPS)	FJ854249	FJ854136	FJ854002
<i>A. fruticosum</i> Benth., acc. 1	Madagascar, <i>P. Phillipson 2082</i> (S)	FJ854250	FJ854137	FJ854003
<i>A. fruticosum</i> , acc. 2	Madagascar, <i>L. Jonsson 1083</i> (UPS)	FJ854251	FJ854138	FJ854004
<i>A. laterale</i> Baker	Malawi, <i>R. K. Brummitt 11554</i> (UPS)	FJ854252	FJ854139	FJ854005
<i>A. parviflorum</i> S. Moore, acc. 1	Uganda, <i>R. A. Dummer 5603</i> (US)	FJ854253	FJ854140	FJ854006
<i>A. parviflorum</i> , acc. 2	Ethiopia, <i>I. Friis et al. 3844</i> (UPS)	FJ854254	FJ854141	FJ854007
<i>A. cf. parviflorum</i> S. Moore	Ethiopia, <i>W. J. J. O. de Wilde & B. E. E. de Wilde-Duyffes 8874</i> (UPS)	FJ854247	FJ854134	FJ854000
<i>A. radicans</i> Gürke	Tanzania, <i>E. Farkas & T. Pocs 86604</i> (UPS)	FJ854255	FJ854142	FJ854008
<i>A. schimper</i> (Briq.) Perkins	Ethiopia, <i>W. Burger 695</i> (US)	FJ854256	FJ854143	FJ854009
<i>Achyrosperrum</i> sp. indet. cf. <i>schimper</i>	Ethiopia, <i>M. Hedren 601</i> (UPS)	FJ854257	FJ854144	FJ854010
<i>Achyrosperrum</i> sp. indet.	Burundi, <i>J. Lewalle 1886</i> (UPS)	FJ854258	FJ854145	FJ854011
<i>Acrotome hispida</i> Benth.	South Africa, <i>P. Herman 1990</i> (C)*	EU138376	EU138299	EU138224
<i>A. inflata</i> Benth.	Namibia, <i>G. L. Maggs & L. Guarino 1072</i> (UPS)*	EU138377	EU138300	EU138225
<i>A. pallescens</i> Benth.	Namibia, <i>I. Örtendahl 105</i> (UPS)*	EU138379	EU138302	EU138226
<i>Anisomeles indica</i> (L.) Kuntze	Pakistan, <i>E. Emanuelsson 2027</i> (S)	FJ854259	FJ854146	FJ854012
<i>A. malabarica</i> (L.) Sims	Sri Lanka, <i>Fagerlind & Klackenberg 343</i> (S)	FJ854260	FJ854147	FJ854013
<i>Ballota acetabulosa</i> (L.) Benth.	Greece, <i>M. Bendiksby & A.-C. Scheen 0412</i> (O)*	EU138342	EU138365	EU138296
<i>B. africana</i> (L.) Benth.	South Africa, <i>K. Bremer 247</i> (S)	FJ854261	FJ854148	FJ854014
<i>B. aucheri</i> Boiss.	Iran, <i>S. Sabaghi s.n., 02.06.1993</i> (S)	FJ854262	FJ854149	FJ854015
<i>B. integrifolia</i> Benth.	Cyprus, <i>H. Lindberg s.n., 11.06.1939</i> (S)	FJ854263	FJ854150	FJ854016
<i>B. nigra</i> L. subsp. <i>ruderalis</i> (Sw.) Briq.	Greece, <i>M. Bendiksby & A.-C. Scheen 0431</i> (O)	FJ854264	FJ854151	FJ854017
<i>B. pseudodictamnus</i> (L.) Benth.	Greece, <i>M. Bendiksby & A.-C. Scheen 0420</i> (O)*	EF546935	EF546857	EU138295
<i>B. undulata</i> (Fresen.) Benth.	Jerusalem, <i>I. Amdursky 1628678</i> (US)	FJ854265	FJ854152	FJ854018
<i>Betonica alopecuroides</i> L.	Italy, <i>S. Vautier 2661390</i> (US)	FJ854308	FJ854203	FJ854088
<i>B. macrantha</i> K. Koch	Georgia, <i>D. McNeal et al. 161</i> (C)	FJ854266	FJ854153	FJ854019
<i>B. macrostachya</i> Wender.	Turkey, <i>P. H. Davis & Hedge 31895</i> (C)	FJ854320	FJ854221	FJ854106
<i>B. officinalis</i> L.	cultivar, <i>C. Lindqvist & V. A. Albert 357</i> (UNA)*	AF502056	FJ854224	FJ854109
<i>B. scardica</i> Griseb., acc. 1	Greece, <i>J. Ugelvig & L. S. Christiansen 1048</i> (C)	FJ854326	FJ854229	FJ854114
<i>B. scardica</i> , acc. 2	Greece, <i>J. Ugelvig & L. S. Christiansen 1051</i> (C)	FJ854327	FJ854230	FJ854115
<i>Bostrychanthera deflexa</i> Benth.	China, <i>Sino-American Guizhou Bot. Exped. 1923</i> (A)	FJ854267	FJ854154	FJ854020
<i>Brazoria arenaria</i> Lundell	U.S.A., <i>M. W. Turner 25</i> (TEX)*	EF546967	EF546890	FJ854021
<i>Chaiturus marrubiastrum</i> (L.) Spenn.	Germany, <i>A. Pedersen 14</i> (C)	FJ854268	FJ854155	FJ854022
<i>Chamaesphecos ilicifolius</i> Schrenk	Iran, <i>K. H. Rechinger 50961</i> (C)	FJ854269	FJ854156	FJ854023
<i>Chelonopsis longipes</i> Makino	Japan, <i>S. Okuyama & N. Maruyama s.n., Nov. 1951</i> (UPS)*	EF546938	EF546861	FJ854024
<i>C. moschata</i> Miq.	cultivar, <i>P. D. Cantino 1429</i> (BHO)	FJ854270	FJ854157	FJ854025

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron
<i>Colquhounia coccinea</i> Wall.	Nepal, S. Einarsson et al. s.n., 29 May 1973 (UPS)*	EF546936	EF546858	FJ854026
<i>C. elegans</i> Wall.	Thailand, C. F. van Beusekom & C. Phengkklai 3008 (C)*	EF546937	EF546859	FJ854027
<i>Comanthosphace formosana</i> Ohwi	Taiwan, Cien-chang Hsu 5824 (S)	FJ854271	FJ854158	FJ854028
<i>C. japonica</i> (Miq.) S. Moore, acc. 1	Japan, M. Ono & S. Kobayashi 45908 (S)	FJ854272	FJ854159	FJ854029
<i>C. japonica</i> , acc. 2	Japan, Shigetaka Suzuki 406009 (US)	FJ854274	FJ854161	FJ854031
<i>C. stellipila</i> (Miq.) Briq.	Japan, T. Shimizu 12869 (S)	FJ854273	FJ854160	FJ854030
<i>Craniotome furcata</i> (Link) Kuntze	Nepal, O. Polunin et al. 5638 (UPS)	FJ854275	FJ854162	FJ854032
<i>Eremostachys laciniata</i> (L.) Bunge	Jordan, M. Kocher B-200 (US)	FJ854276	FJ854163	FJ854033
<i>Eriophyton wallichii</i> Benth.	Nepal, Stainton et al. 7748 (UPS)	FJ854277	FJ854164	FJ854034
<i>Galeopsis angustifolia</i> Hoffm.	France, E. Dahl s.n., 26 Aug. 1979 (O)*	EF546939	EF546862	FJ854035
<i>G. pubescens</i> Besser	Poland, T. Tacik & M. Sychowa 366 (O)*	EF546940	EF546863	FJ854036
<i>G. speciosa</i> Mill.	Norway, T. Berg 04-01 (O)	FJ854278	FJ854165	FJ854037
<i>Gomphostemma javanicum</i> (Blume) Benth.	unknown, R. G. Olmstead 93-38*	AF502028	EF546860	FJ854038
<i>Haplostachys haplostachya</i> (A. Gray) H. St. John	Hawaii, S. Perlman 14328 (NY)*	AF502029	FJ854166	FJ854039
<i>Isoleucas arabica</i> O. Schwartz	Yemen, M. Thulin et al. 8402 (UPS)*	EU138380	EU138303	EU138227
<i>I. somala</i> (Patzak) Scheen	Somalia, M. Thulin & A. M. Warfa 5395 (UPS)*	EU138439	EU138362	EU138285
<i>Lagochilus cabulicus</i> Benth.	Pakistan, E. Emanuelsson 2456 (S)	FJ854279	FJ854167	FJ854040
<i>L. hirtus</i> Fisch. & C. A. Mey.	Kazakhstan, I. O. Baitulin et al. s.n., 18 Sep. 1997 (UPS)	FJ854280	FJ854168	FJ854041
<i>L. ilicifolius</i> Benth.	Mongolia, T. Norlindeh & T. Ahti 29330 (S)	FJ854281	FJ854169	FJ854042
<i>Lamiastrum montanum</i> (Pers.) Ehrend.	Austria, W. Till s.n., 24 May 1998 (WU)	FJ854282	FJ854170	FJ854043
<i>Lamium album</i> L. subsp. <i>crinatum</i> (Monbret & Aucher ex Benth.) Mennema	Iran, J. Bornmüller 7947 (WU)*	EF546932	EF546854	FJ854044
<i>L. tomentosum</i> Willd.	Russia, J. Klackenberg 820620-27 (S)*	EF546933	EF546855	EU138293
<i>Leonotis leonurus</i> (L.) R. Br.	South Africa, F. Venter & P. Vorster 171 (US)*	EU138382	EU138305	EU138229
<i>L. myricifolia</i> Iwarsson & Y. B. Harv.	Malawi, M. Iwarsson & O. Ryding 986 (UPS)*	EU138383	EU138306	EU138230
<i>L. nepetifolia</i> (L.) R. Br. var. <i>nepetifolia</i>	Tanzania, R. Abdallah et al. 493 (UPS)*	EU138386	EU138309	EU138233
<i>L. ocyimifolia</i> (Burm. f.) Iwarsson var. <i>schinzii</i> (Gürke) Iwarsson	Botswana, R. Blomberg et al. 713 (UPS)*	EU138389	EU138312	EU138236
<i>Leonurus sibiricus</i> L.	Argentina, T. M. Pedersen 16317 (UPS)*	EF546930	EF546852	FJ854045
<i>L. turkestanicus</i> V. I. Krecz. & Kuprian.	Kazakhstan, I. Roldugin & V. Fissjun 5393 (S)*	EF546931	EF546853	FJ854046
<i>Leucas aspera</i> (Willd.) Link	Thailand, O. Ryding 697 (UPS)*	EU138395	EU138318	EU138242
<i>L. bijflora</i> (Vahl) Sm.	Sri Lanka, M. Iwarsson 610 (UPS)*	EU138396	EU138319	EU138243
<i>L. calostachys</i> Oliv.	Kenya, M. Iwarsson 280 (UPS)*	EU138398	EU138321	EU138245
<i>L. deflexa</i> Hook. f. var. <i>deflexa</i>	Tanzania, A. Hemp 4285 (O)*	EU138403	EU138326	EU138250
<i>L. flagellifera</i> (Balf. f.) Gürke	Yemen, Socotra, M. Thulin & A. N. Gifri 8750 (UPS)*	EU138406	EU138329	EU138253
<i>L. glabrata</i> (Vahl) Sm.	Ethiopia, O. Ryding 2351 (UPS)*	EU138407	EU138330	EU138254
<i>L. inflata</i> Benth.	Ethiopia, M. Thulin et al. 3869 (UPS)*	EU138410	EU138333	EU138257
<i>L. jamesii</i> Baker	Somalia, O. Hedberg et al., Somalia Medicinal Plant Project 85 (UPS)*	EU138411	EU138334	EU138258

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron
<i>L. lanata</i> Benth.	Nepal, <i>Stainton et al.</i> 661 (UPS)*	EU138413	EU138336	EU138260
<i>L. lavandulifolia</i> Sm.	Palau, <i>C. A. Salsedo</i> 164 (US)*	EU138414	EU138337	EU138261
<i>L. martinicensis</i> (Jacq.) R. Br.	Ethiopia, <i>O. Ryding et al.</i> 2190 (UPS)*	EU138416	EU138339	EU138263
<i>L. minimifolia</i> Chiov.	Somalia, <i>M. Thulin & A. M. Dahir</i> 6706 (UPS)*	EU138419	EU138342	EU138266
<i>L. sexdentata</i> Skan	Botswana, <i>O. Ryding</i> 2310 (UPS)*	EU138424	EU138347	EU138271
<i>L. spiculifolia</i> (Balf. f.) Gürke	Yemen, Socotra, <i>M. Thulin & A. N. Gifri</i> 8688 (UPS)*	EU138425	EU138348	EU138272
<i>L. stachydiformis</i> (Benth.) Briq.	Ethiopia, <i>K. Hylander et al.</i> 97 (UPS)*	EU138426	EU138349	EU138273
<i>L. urticifolia</i> (Vahl) Sm. var. <i>urticifolia</i>	Eritrea, <i>O. Ryding & Sileshi N.</i> 1763 (UPS)*	EU138427	EU138350	EU138274
<i>Leucosceptrum canum</i> Sm.	Nepal, <i>C. T. Mason Jr. & P. B. Mason</i> 3963 (US)	FJ854283	FJ854171	FJ854047
<i>Marrubium alysson</i> L.	Italy, <i>M. H. G. Gustafsson s.n.</i> , 5 Apr. 1990 (UPS)	FJ854284	FJ854172	FJ854048
<i>M. peregrinum</i> L.	Greece, <i>A. Strid</i> 33875 (C)	FJ854285	ND	FJ854049
<i>M. thessalum</i> Boiss. & Heldr.	Greece, <i>S. & B. Snogerup</i> 15993 (UPS)	FJ854286	FJ854173	FJ854050
<i>M. vulgare</i> L.	Saudi Arabia, <i>I. & O. Hedberg</i> 92075 (UPS)*	EU138443	EU138366	EU138294
<i>Melittis melisophyllum</i> L.	Hungary, <i>M. E. Steiner et al.</i> 1127 (UPS)*	EF546929	EF54849	FJ854051
<i>Microtoena patchoulī</i> (C. B. Clarke ex Hook. f.) C. Y. Wu & S. J. Hsuan	China, <i>H. Y. Liang</i> 66028 (US)	FJ854287	FJ854174	FJ854052
<i>Moluccella aucheri</i> (Boiss.) Scheen, acc. 1	Pakistan, <i>G. Popov</i> 123 (C)*	EU138446	EU138369	FJ854053
<i>M. aucheri</i> , acc. 2	Pakistan, <i>K. H. Rechinger</i> 54859 (S)*	EU138447	EU138370	FJ854054
<i>M. laevis</i> L.	U.S.A., <i>W. C. Brumbach</i> 7249 (S)*	EU138444	EU138367	FJ854055
<i>M. spinosa</i> L.	Spain, <i>Laza s.n.</i> , 16 June 1935 (S)*	EU138445	EU138368	FJ854056
<i>Notochaete hamosa</i> Benth.	Nepal, <i>Stainton et al.</i> 3649 (UPS)	FJ854288	FJ854175	FJ854057
<i>Otostegia erlangeri</i> Gürke	Ethiopia, <i>M. G. Gilbert et al.</i> 7965 (UPS)*	EU138432	EU138355	EU138279
<i>O. fruticosa</i> (Forssk.) Schweinf. ex Lenzig	Saudi Arabia, <i>I. & O. Hedberg</i> 92184 (UPS)*	EU138433	EU138356	EU138280
<i>O. modesta</i> S. Moore	Ethiopia, <i>M. G. Gilbert & D. Sebsebe</i> 8631 (UPS)*	EU138437	EU138360	EU138283
<i>Panzerina lanata</i> (L.) Soják, acc. 1	Russia, <i>V. Reverdatto s.n.</i> , 24 July 1927 (S)	FJ854289	FJ854176	FJ854058
<i>P. lanata</i> , acc. 2	Mongolia, <i>T. Norlindh & T. Ahti</i> 10044 (S)	FJ854290	FJ854177	FJ854059
<i>Paraphlomis javanica</i> (Blume) Prain, acc. 1	China, <i>Sino-American Guizhou Bot. Exped.</i> 1262 (A)	FJ854291	ND	FJ854060
<i>P. javanica</i> , acc. 2	Thailand, <i>J. F. Rock</i> 1097 (US)	FJ854292	FJ854178	FJ854061
<i>Phlomidioschema parviflorum</i> (Benth.) Vved.	Afghanistan, <i>J. S. Andersen & I. C. Petersen</i> 394 (C)	FJ854293	FJ854179	FJ854062
<i>Phlomis fruticosa</i> L.	Greece, <i>E. Julin s.n.</i> , 19 Apr. 1985 (UPS)	FJ854294	FJ854180	FJ854063
<i>P. milingensis</i> C. Y. Wu & H. W. Li	Garden material, <i>C. Mathiesen & J. M. Taylor</i> 17 (O)*	EU138448	EU138371	EU138292
<i>P. purpurea</i> L.	<i>M. Thulin et al.</i> 4782 (UPS)*	EU138449	EU138372	EU138291
<i>P. tuberosa</i> L.	Garden material, <i>C. Mathiesen & J. M. Taylor</i> 88 (O)	FJ854295	FJ854181	FJ854064
<i>Phyllostegia glabra</i> (Gaudich.) Benth.	Hawaii, <i>K. Wood</i> 3962 (NY)*	AF502031	FJ854182	FJ854065

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron
<i>Physostegia intermedia</i> (Nutt.) Engelm. & A. Gray	U.S.A., R. Dale Thomas 88861 (US)*	EF546948	EF546871	FJ854066
<i>P. virginiana</i> (L.) Benth.	U.S.A., B. E. Wofford 88-12 (US)*	EF546961	EF546884	FJ854067
<i>Pogostemon glaber</i> Benth.	Nepal, Stainton et al. 8327 (UPS)	FJ854296	FJ854183	FJ854068
<i>P. heyneanus</i> Benth.	Sri Lanka, J. Klackenberg 100 (S)	FJ854297	FJ854184	FJ854069
<i>P. hirsutus</i> Benth.	Sri Lanka, J. Klackenberg 51 (S)	FJ854298	FJ854185	FJ854070
<i>P. paniculatus</i> (Willd.) Benth.	India, J. Klackenberg & R. Lundin 565 (S)	FJ854299	FJ854186	FJ854071
<i>Prasium majus</i> L.	Spain, M. Thulin 5752 (UPS)	FJ854300	FJ854187	FJ854072
<i>Pseuderemostachys sewerzovii</i> (Herder) Popov	Kazakhstan, N. Karmysheva s.n., 12 May 1962 (C)	FJ854301	FJ854188	FJ854073
<i>Rostrinucula dependens</i> (Rehder) Kudô	China, D. E. Boufford et al. 24415 (A)	FJ854302	FJ854189	FJ854074
<i>R. sinensis</i> (Hemsl.) C. Y. Wu	China, Sino-American Guizhou Bot. Exped. 40 (A)	FJ854303	FJ854190	FJ854075
<i>Roylea cinerea</i> (D. Don) Baill.	Nepal, O. Polunin et al. 837 (UPS)*	EU138450	EU138373	EU138290
<i>Rydingia integrifolia</i> (Benth.) Scheen & V. A. Albert	Yemen, M. Thulin et al. 8161 (UPS)*	EU138435	EU138358	EU138282
<i>R. persica</i> (Burm. f.) Scheen & V. A. Albert	Iran, K. Nikookar s.n., 9 Sep. 1963 (S)*	EU138438	EU138361	EU138284
<i>Sideritis dasygnaphala</i> (Webb & Berthel.) Clos	Canary Islands, J. Barber 196 (TEX)*	AF501993	FJ854191	FJ854076
<i>S. gomerae</i> Bolle subsp. <i>gomerae</i>	Canary Islands, J. Barber 256 (TEX)*	AF502036	FJ854192	FJ854077
<i>S. hyssopifolia</i> L.	Spain, J. Barber 202 (TEX)*	AF502037	FJ854193	FJ854078
<i>S. macrostachys</i> Poir.	Canary Islands, J. Barber 254 (TEX)*	AF502038	FJ854194	FJ854079
<i>S. montana</i> L.	Romania, J. Barber 212 (TEX)*	AF502039	FJ854195	FJ854080
<i>S. romana</i> L.	Italy, J. Barber 209 (TEX)*	AF502040	FJ854196	FJ854081
<i>S. syriaca</i> L., acc. 1	Greece, J. Barber 210 (TEX)*	AF335659	FJ854197	FJ854082
<i>S. syriaca</i> , acc. 2	Greece, M. Bendiksy & A.-C. Scheen 0408 (O)	FJ854304	FJ854198	FJ854083
<i>Stachys aculeolata</i> Hook. f.	Kenya, Y. B. Harvey et al. s.n., 24 Oct. 1992 (C)	FJ854305	FJ854199	FJ854084
<i>S. aethiopica</i> L.	Mozambique, B. Pettersson 2146 (UPS)	FJ854307	FJ854201	FJ854086
<i>S. affinis</i> Bunge	cultivar, C. Lindqvist & V. A. Albert 359 (UNA)*	AF502041	FJ854202	FJ854087
<i>S. alpigena</i> T. C. E. Fr.	Ethiopia, O. Ryding 2133 (UPS)	FJ854309	FJ854204	FJ854089
<i>S. arabica</i> Hornem.	Israel, I. Gruenberg 685 (UPS)	FJ854312	FJ854207	FJ854092
<i>S. argillicola</i> Sebsebe	Ethiopia, I. Friis et al. 3104 (C)*	AF502044	FJ854208	FJ854093
<i>S. arensis</i> (L.) L.	Canary Islands, N. Lundqvist 8157 (UPS)	FJ854313	FJ854209	FJ854094
<i>S. byzantina</i> K. Koch	cultivar, C. Lindqvist & V. A. Albert 356 (UNA)*	AF502046	FJ854211	FJ854096
<i>S. cassia</i> (Boiss.) Boiss.	Greece, S. & B. Snogerup 14974 (UPS)	FJ854315	FJ854212	FJ854097
<i>S. chamissonis</i> Benth.	U.S.A., H. N. Moldenke et al. 32097 (LL)*	AF502050	FJ854213	FJ854098
<i>S. coccinea</i> Ortega	cultivar, C. Lindqvist & V. A. Albert 355 cult. 911/97A (NYBC)*	AF502048	FJ854214	FJ854099
<i>S. cretica</i> L.	Greece, A. Strid et al. 42603 (C)	FJ854316	FJ854215	FJ854100
<i>S. debilis</i> Kunth	Ecuador, C. Jativa & C. Epling 242 (US)	FJ854317	FJ854216	FJ854101
<i>S. graeca</i> Boiss. & Heldr.	Greece, K. H. Rechinger 16887 (US)	FJ854306	FJ854200	FJ854085
<i>S. grandidentata</i> Lindl.	Chile, W. J. Eyerdam 10081 (US)	FJ854318	FJ854217	FJ854102
<i>S. hyssopoides</i> Benth.	South Africa, E. Retief 1080 (US)	FJ854319	FJ854218	FJ854103
<i>S. laxandulifolia</i> Vahl	Iran, J. S. Andersen & A. G. Jensen 7032 (C)*	AF502053	FJ854219	FJ854104

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron
<i>S. lindenii</i> Benth.	Mexico, <i>R. Torres C. & P. Tenorio L. 4602</i> (TEX)*	AF502054	FJ854220	FJ854105
<i>S. maritima</i> Gouan	Romania, <i>I. Gergely 3362</i> (US)	FJ854321	FJ854222	FJ854107
<i>S. nephrophylla</i> Rech. f.	Iraq, <i>K. H. Rechinger 11250</i> (WU)	FJ854322	FJ854223	FJ854108
<i>S. pilosa</i> Nutt.	U.S.A., <i>H. Hapeman s.n.</i> , 30 July 1938 (UPS)	FJ854311	FJ854206	FJ854091
<i>S. plumosa</i> Griseb.	Greece, <i>S. & B. Snogerup 15337</i> (UPS)	FJ854310	FJ854205	FJ854090
<i>S. quercetorum</i> A. Heller	U.S.A., <i>G. K. Helmkamp et al. 2153</i> (UTC)*	AF502042	FJ854225	FJ854110
<i>S. recta</i> L.	Austria, <i>P. Schönswetter 2517</i> (WU)	FJ854323	FJ854226	FJ854111
<i>S. recta</i> subsp. <i>subcrenata</i> (Vis.) Briq.	Croatia, <i>G. Schneewis et al. 6268</i> (WU)	FJ854330	FJ854233	FJ854118
<i>S. riederi</i> Cham.	Japan, <i>H. Takahashi 2950</i> (C)	FJ854314	FJ854210	FJ854095
<i>S. rotundifolia</i> Benth.	Mexico, <i>D. E. Breedlove 55575</i> (TEX)	FJ854324	FJ854227	FJ854112
<i>S. rugosa</i> Aiton	South Africa, <i>W. J. Hanekom 2487</i> (US)	FJ854325	FJ854228	FJ854113
<i>S. setifera</i> C. A. Mey.	Iran, <i>J. S. Andersen & I. C. Petersen 115</i> (C)	FJ854328	FJ854231	FJ854116
<i>S. spinosa</i> L.	Greece, <i>M. Bendiksy & A.-C. Scheen 0422</i> (O)	FJ854329	FJ854232	FJ854117
<i>S. swainsonii</i> Benth.	Greece, <i>A. Strid et al. 39692</i> (C)*	AF502062	FJ854234	FJ854119
<i>S. sylvatica</i> L.	cultivar, <i>C. Lindqvist & V. A. Albert 358</i> (UNA)*	AF502063	FJ854235	FJ854120
<i>Stenogyne rugosa</i> Benth.	Hawaii, <i>C. Lindqvist & V. A. Albert 40</i> (NY)*	AF502067	FJ854236	FJ854121
<i>Suzukia luchuensis</i> Kudô	Japan, <i>S. Tawada & S. Hatusima 18179</i> (US)	FJ854331	FJ854237	FJ854122
<i>S. shikikunensis</i> Kudô	Taiwan, <i>C.-C. Liao et al. 564</i> (A)	FJ854332	FJ854238	FJ854123
<i>Synandra hispidula</i> (Michx.) Baill.	U.S.A., <i>V. E. McNeill 97-143</i> (GH)*	EF546970	EF546893	FJ854124
<i>Thuspeinanta brahuica</i> (Boiss.) Briq.	Iran, <i>K. H. & F. Rechinger 4701</i> (US)	FJ854333	FJ854239	FJ854125
<i>T. persica</i> (Benth.) Briq.	Iraq, <i>K. H. Rechinger 9604</i> (S)	FJ854334	FJ854240	FJ854126
<i>Warnockia scutellarioides</i> (Engelm. & A. Gray) M. W. Turner	U.S.A., <i>M. H. Mayfield & G. Nesom 1970</i> (US)*	EF546971	EF546894	FJ854127
<i>Wiedemannia multifida</i> (L.) Benth.	Turkey, <i>J. & F. Bornmüller 14536</i> (S)	FJ854335	FJ854241	FJ854128
Outgroup				
<i>Callicarpa americana</i> L.	cultivar, <i>K-0818400507</i> (K)*	AJ505535	AJ505535	AJ505412
<i>C. japonica</i> Thunb.	cultivar, <i>K-1934-12904</i> (K)*	AJ505536	AJ505536	AJ505413
<i>Congea tomentosa</i> Roxb.	<i>Wagstaff s.n.</i> (BHO)*	AJ505530	AJ505530	AJ505411
<i>Cymaria acuminata</i> Decne.	<i>O. Philipp 446</i> (UPS)	FJ854244	FJ854131	FJ853997
<i>C. dichotoma</i> Benth.	China, <i>C. Wang 33150</i> (US)	FJ854245	FJ854132	FJ853998
<i>Elsholtzia stauntonii</i> Benth.	<i>Wagstaff 356</i> (BHO)*	AJ505526	AJ505526	AJ505406
<i>Gmelina hystrix</i> Schult. ex Kurz	cultivar, <i>K-381-74-02999</i> (K)*	AJ505527	AJ505527	AJ505407
<i>Haumaniastrum katangense</i> (S. Moore) J. Duvign. & Plancke	cultivar, <i>K-1995-1197, Chase 13330</i> (K)*	AJ505540	AJ505540	AJ505417
<i>Hyperia macrantha</i> (Benth.) Harley	<i>Atkinson & Giorgio 150</i> (K)*	AJ505445	AJ505445	AJ505336
<i>Isodon coetsa</i> (Buch.-Ham. ex D. Don) Kudô	<i>Suddee et al. 1085</i> (BKF, K, TCD)*	AJ505454	AJ505454	AJ505342
<i>Lantana camara</i> L.	<i>C. Vazquez Yanes 526</i> (GB)*	AF231884	AF231884	AF225294
<i>Lavandula buchii</i> Webb & Berthel.	<i>Upson 299</i> (RNG)*	AJ505460	AJ505460	AJ505346
<i>Melissa officinalis</i> L.	<i>Wagstaff 88-09</i> (BHO)*	AJ505529	AJ505529	AJ505410
<i>Nepeta fissa</i> C. A. Mey.	<i>Jamzad & Nikchreh 80486</i> (TARI)*	AJ505430	AJ505430	AJ505323
<i>Origanum vulgare</i> L.	cultivar, <i>K-000-69-19317, Chase 13334</i> (K)*	AJ505543	AJ505543	AJ505422

Table 1. Continued.

Taxon	Origin/voucher information	GenBank accession no.		
		<i>trnL</i> intron	<i>trnL-F</i> spacer	<i>rps16</i> intron
<i>Platostoma annamense</i> (G. Taylor) A. J. Paton	Suddee et al. 1028 (BKF)*	AJ505479	AJ505479	AJ505361
<i>Plectranthus buchananii</i> Baker	cultivar, K-1970-3559, Brummitt 11597 (K)*	AJ505501	AJ505501	AJ505379
<i>P. helferi</i> Hook. f.	Chase 9768 (K)*	AJ505552	AJ505552	AJ505429
<i>Prostanthera nivea</i> Benth.	M. W. Chase 6980 (K)*	AJ505524	AJ505524	AJ505403
<i>P. petrophila</i> B. J. Conn	M. W. Chase 6975 (K)*	AJ505525	AJ505525	AJ505404
<i>Pycnostachys reticulata</i> (E. Mey.) Benth.	cultivar, K-1999-2425, Nat. Bot. Gar. S. Africa (K)*	AJ505516	AJ505516	AJ505395
<i>Salvia guaranitica</i> A. St.-Hil. ex Benth.	cultivar, K-1973-14217 (K)*	AJ505549	AJ505549	AJ505421
<i>Scutellaria hirta</i> Sm.	Greece, M. Bendiksby & A.-C. Scheen 0411 (O)*	EF546927	EF546847	EU138289
<i>S. sieberi</i> Benth.	Greece, M. Bendiksby & A.-C. Scheen 0418 (O)*	EF546928	EF546848	EU138288
<i>Tectona grandis</i> L. f.	Waimea 73P172*	AJ505528	AJ505528	AJ505408
<i>Teucrium alpestre</i> Sm.	Greece, M. Bendiksby & A.-C. Scheen 0426 (O)	AJ854242	AJ854129	AJ853995
<i>T. scorodonia</i> L.	Norway, A.-C. Scheen 0412 (O)	AJ854243	AJ854130	AJ853996
<i>Thymus serpyllum</i> L. var. <i>citriodorus</i> (Schreb.) Becker	cultivar, K-1975-1177, Chase 13331 (K)*	AJ505544	AJ505544	AJ505423
<i>Verbena officinalis</i> L.	H. Kalheber 78-506 (GB)*	AF231885	AF231885	AF225295
<i>Vitex trifolia</i> L.	TCMK 15, Chase 8757 (K)*	AJ505539	AJ505539	AJ505416

ND, sequences not determined.

* Sequences that were not new to this study were retrieved from GenBank and were originally published by Lindqvist and Albert (2002), Paton et al. (2004), Wallander and Albert (2000), Scheen et al. (2008), or Scheen and Albert (2009).

the analysis, using the data matrix without indels coded, were: general time reversible model, estimated gamma shape parameter = 1.36, four substitution rate categories, empirically derived equilibrium state frequencies ($\{[A] = 0.34185$, $\{[C] = 0.16969$, $\{[G] = 0.18884$, $\{[T] = 0.29961$), empirically derived proportion of invariant sites = 0.164, starting tree determined by BIONJ neighbor-joining (Gascuel, 1997), and tree optimization using nearest neighbor interchange (NNI) rearrangements. Using the same web server, a bootstrap analysis of 100 replicates was performed to estimate internal robustness of the data.

TAXONOMY

Only monophyletic groups were selected for suprageneric Linnaean classification of Lamiioideae. The criterion used was to circumscribe entities at the tribal level (mostly with high jackknife support [JAC] > 80%) that would be practical at present, with no attempt made to classify every clade that could have equivalent hierarchical status. In order to avoid phylogenetic redundancy, no monogeneric tribes were

circumscribed at this time, although in some cases they may occupy key phylogenetic positions. No subtribal names were proposed, principally because morphological characteristics rendered this impractical (e.g., within tribe Pogostemoneae Briq. and tribe Stachydeae Dumort.). Names for tribes were selected following the rules of the *International Code of Botanical Nomenclature* (McNeill et al., 2006). Authorship, priority, and valid publication of names were determined by examining original publications and by consulting several sources (Sanders & Cantino, 1984; Reveal, 2007, pers. comm.; Govaerts et al., 2010; International Plant Names Index, 2010).

RESULTS AND DISCUSSION

Alignment of the 197 Lamiaceae and Verbenaceae *trnL-F* sequences resulted in a data matrix of 1241 characters, including indels and missing data. With simple indel coding in SeqState, 253 indels were coded as present or absent (or missing), increasing the matrix size to 1494 characters. The *rps16* matrix had an aligned length of 1201 bp including indels and

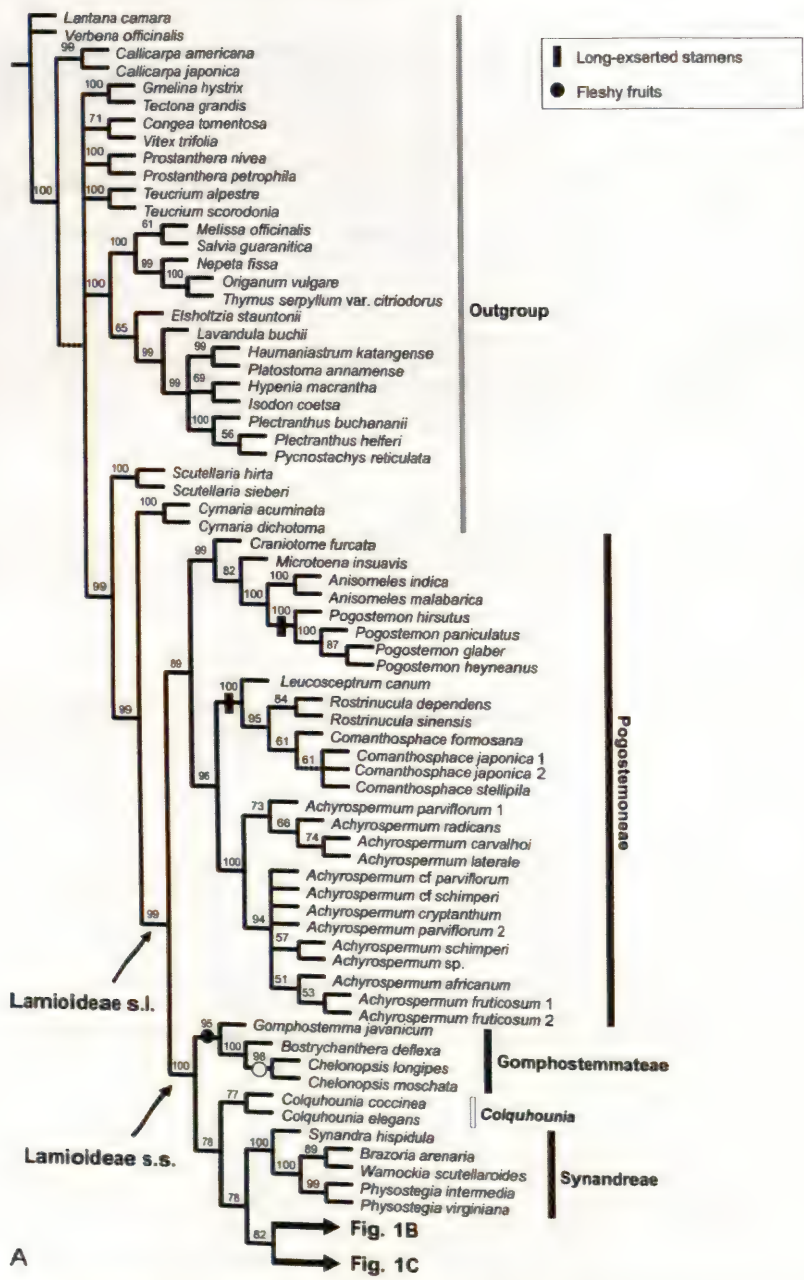


Figure 1. Strict consensus of 256 MPTs from a parsimony analysis of an indel-coded and concatenated matrix of the *trnL-F* region and *rps16* intron. Jackknife values are given above branches. Branches that collapsed in the strict consensus of 1728 MPTs resulting from a parsimony analysis where indels that were not coded are shown as stippled lines. Major clades are named following the proposed new suprageneric classification of Lamioideae s.l. —A. Outgroups, *Colquhounia* Wall., and *Paraphlomis* (Prain) Prain, *Roylea* Wall. ex Benth., *Galeopsis* L., *Betonica* L., and tribe Stachydeae. —C. Marrubieae, and Leucadeae. Non-Stachys taxa nested within tribe Stachydeae (B) are in boldface. Clades A–D are referred to shapes on the figure: origin in black, reversal in white (see Issues in Lamioideae Character Evolution). Note that *Leucas sexdentata* phylogenetic resolution among the three *Acrotome* species and *L. sexdentata*.

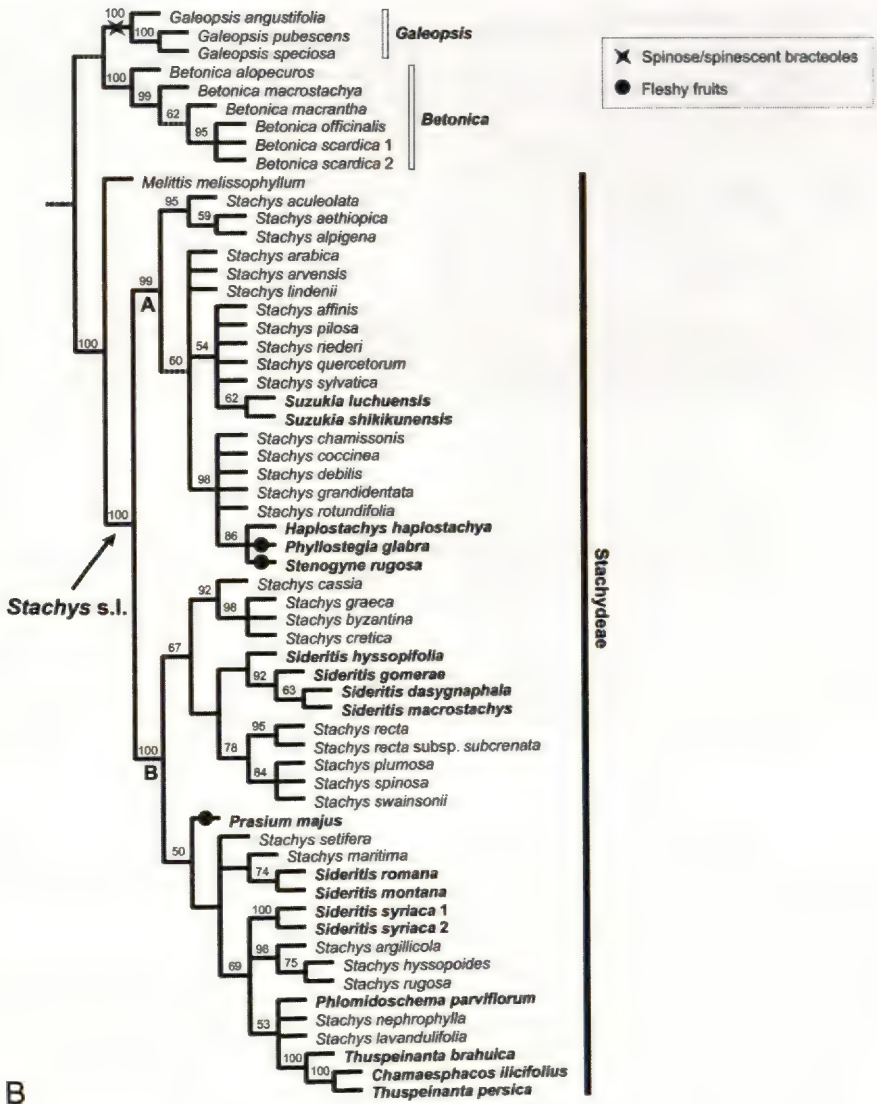
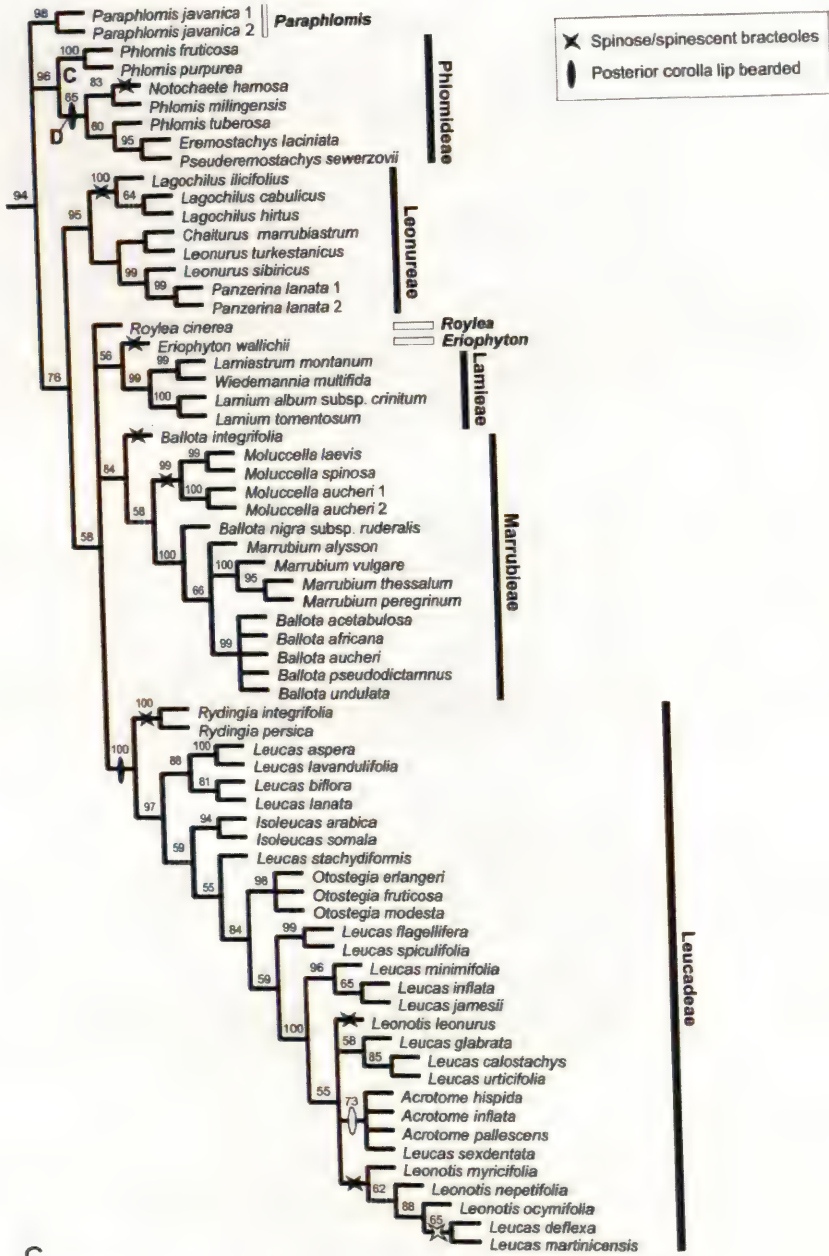


Figure 1. Continued.

missing data. SeqState coded 192 indels, which increased the matrix size to 1393 characters. The concatenated matrix had 2442 characters when indels were not coded and 2887 characters when indels were coded and included as binary characters. The maximum parsimony analysis of the concatenated matrix resulted in 1728 most parsimonious trees (MPTs) of 2302 steps with a consistency index (CI) of 0.61 and a retention index (RI) of 0.88 when indels were not coded and 256 MPTs of 3103 steps when indels were coded (CI = 0.59, RI = 0.87).

The results of the parsimony analyses with and without indel coding were largely congruent (Fig. 1).

Maximum likelihood analysis yielded an entirely consistent tree with that derived from parsimony, and most of the same branches supported by parsimony analysis were also supported by the maximum likelihood bootstrap results (results not shown). In all analyses, *Cymaria* Benth. was strongly supported (by jackknife and bootstrap resampling) as sister to Lamiioideae plus Pogostemonoideae. This clade was in turn sister to *Scutellaria* L. (representing Scutellarioideae). In all analyses, members of the former subfamily Pogostemonoideae grouped with three members of Lamiioideae (*Achyroserpnum* Blume, *Craniotome* Rehb., and *Microtoena* Prain), which



C

Figure 1. Continued.

therefore rendered subfamily Pogostemonoideae paraphyletic. Lamioideae s. str., a much larger group, formed a well-supported clade. The following major groups within this latter clade were supported (by jackknife and bootstrap resampling) in all analyses: (1) a clade consisting of *Gomphostemma* Wall. ex Benth., *Bostrychanthera* Benth., and *Chelonopsis* Miq.

as sister to the remaining taxa; (2) a clade of the North American genera *Synandra* Nutt., *Brazoria* Engelm. & A. Gray, *Warnockia* M. W. Turner, and *Physostegia* Benth.; (3) the genus *Galeopsis* L.; (4) members of *Stachys* subg. *Betonica* (L.) R. Bhattacharjee; (5) *Melittis* L. sister to a large clade of *Stachys*, *Sideritis*, and a number of smaller or monotypic genera; (6) the

genus *Phlomis*, including members of *Eremostachys* Bunge, *Notochaete* Benth., and *Pseuderemostachys* Popov; (7) *Lagochilus* Bunge ex Benth. sister to the smaller genera *Chaiturus* Willd., *Leonurus* L., and *Panzerina* Soják; (8) the genus *Lamium* L. sister to *Lamiastrum* Heist. ex Fabr. plus *Wiedemannia* Fisch. & C. A. Mey.; (9) a clade of *Ballota* L., *Marrubium* L., and *Moluccella* L.; and (10) a large clade of *Leucas*, *Leonotis* (Pers.) R. Br., *Otostegia* Benth., *Acrotome* Benth. ex Endl., *Rydingia* Scheen & V. A. Albert, and *Isoleucas* O. Schwartz. When indels were coded, *Galeopsis* and members of *Stachys* subg. *Betonica* formed a group, although not supported by resampling, which was sister to the *Melittis*–*Stachys* s.l. group (Fig. 1B).

CIRCUMSCRIPTION OF LAMIOIDEAE

Scutellaria. *Scutellaria* is a large cosmopolitan genus of ca. 360 species belonging to the subfamily Scutellarioideae. This subfamily also includes the genus *Tinnea* Kotschy & Peyr. (ca. 20 spp.) as well as the monotypic genera *Holmskioldia* Retz., *Wenchengia* C. Y. Wu & S. Chow, and *Renschia* Vatke, all of which are Old World tropical. Although Scutellarioideae is represented here by only two *Scutellaria* species and our outgroup sampling is otherwise relatively limited, our results corroborate earlier evidence (Wagstaff & Olmstead, 1997; Wagstaff et al., 1998; Lindqvist & Albert, 2002) for the subfamily being closely related to Lamioideae in the classical sense (i.e., as circumscribed by Harley et al., 2004).

The exact circumscription of Lamioideae still remains a problem. The first issue regards the status of pogostemonoid genera, formerly classified in a separate subfamily, Pogostemonoideae (Cantino et al., 1992). Morphological considerations led Harley et al. (2004) to subsume the pogostemonoids within a larger Lamioideae, and we provide here the first phylogenetic evidence corroborating this view (see below). The second issue actually precedes the first in a phylogenetic sense: the enigmatic genus *Cymaria* is intercalated between Scutellarioideae and Lamioideae plus pogostemonoids.

Cymaria. In all of our phylogenetic analyses, the broader Lamioideae clade is strongly supported as the monophyletic sister group to two accessions of *Cymaria* (99% JAC; Fig. 1A). *Cymaria* is a small genus comprising two to three species from Southeast Asia. *Cymaria* was not classified to a particular subfamily of Lamiaceae by Harley et al. (2004), although suggestions for placement have been made in the past, in part based on the results of a morphological phylogenetic analysis (Cantino et al., 1992).

Other taxa unplaced by Harley et al. (2004) may be relevant to our interesting phylogenetic resolution of *Cymaria*. Cantino et al.'s (1992) classification, now superseded by Harley et al. (2004), placed *Cymaria* in a group together with the monotypic genera *Acrymia* Prain, *Garrettia* H. R. Fletcher, and *Holocheila* (Kudô) S. Chow, all occurring in areas of southeastern Asia. *Cymaria* shares a distinctive inflorescence structure with *Acrymia* and *Garrettia* (Harley et al., 2004: 189) and palynological similarity with *Garrettia* (Abu-Asab & Cantino, 1994), whereas other morphological features link *Holocheila* with Scutellarioideae (see Harley et al., 2004: 189–190). However, DNA data appear to place *Holocheila* within Lamioideae (R. G. Olmstead, unpubl. data; see Harley et al., 2004: 190), while phylogenetic studies of *ndhF* cpDNA sequences corroborate that *Cymaria* is sister to the Lamioideae clade (R. G. Olmstead, pers. comm.). One possible link between these taxa and pogostemonoid taxa may be inflorescences with prominently pedunculate cymes, a trait that is also seen in *Craniotome* and *Microtoena*. However, more data are required, especially from the tropical East Asian monotypic genera *Acrymia*, *Garrettia*, and *Holocheila* (none of which could be included here), in order to assess the possibility of assigning *Cymaria* and perhaps some of the other genera to Lamioideae or to a subfamily of their own.

TRIBE POGOSTEMONEAE

As stated above, our molecular phylogeny confirms the morphologically based view that lamiod and pogostemonoid taxa are intermingled, and in fact together form a highly supported monophyletic group (99% JAC; Fig. 1A). Previous phylogenetic studies did not succeed in verifying the status of Lamioideae and Pogostemonoideae as separate taxa. Only two cladistic treatments have included more than one representative of Pogostemonoideae (Cantino, 1992a; Wagstaff et al., 1998). In Wagstaff et al. (1998), Lamioideae and Pogostemonoideae were monophyletic sister taxa, although the pogostemonoid clade only received low bootstrap support. In Cantino (1992a), Pogostemonoideae was sister to a Lamioideae–*Nepe-toideae* clade. However, in our analyses, which are much better sampled, there is no support for a monophyletic subfamily Pogostemonoideae.

The pogostemonoid labiates fall into two separate groups that, together with three genera of subfamily Lamioideae (*Achyrosperrum*, *Craniotome*, and *Microtoena*), form a highly supported group (89% JAC; Fig. 1A). The two pogostemonoid genera *Anisomeles* R. Br. (three spp.) and *Pogostemon* Desf. (ca. 80 spp.) are sister taxa with high support (100% JAC), corroborating the results of previous morphological

studies by Cantino (1992a, b). A close relationship between these two genera had never been suggested prior to Cantino's work. However, Briquet (1895–1897) grouped *Anisomeles* with *Achyropermum*, *Craniotome*, and *Microtoena*, but did not recognize their close relationship to *Pogostemon* (Fig. 1A). In all our analyses, *Anisomeles* and *Pogostemon* group with monotypic *Craniotome* and *Microtoena* (24 spp.) with high support (99% JAC). All species within this clade are mostly tropical East Asian, although *Anisomeles* species also occur in the West Indian Ocean and *Pogostemon* in Africa, and *Craniotome* and *P. glaber* Benth. reach the Himalayas.

The monotypic *Leucosceptrum* Sm., *Comanthosphace* S. Moore (three to four spp.), and *Rostrinucula* Kudô (two spp.) form another highly supported clade (100% JAC) within which *Comanthosphace* and *Rostrinucula* are well supported as sister taxa (99% JAC). This group is also primarily tropical East Asian, with some species reaching temperate East Asia, and *Leucosceptrum* reaching the Himalayas. These three pogostemonoid genera are highly supported as sister to the lamioid genus *Achyropermum* (ca. 25 spp.) in all analyses (96% JAC; Fig. 1A). Although only African representatives of *Achyropermum* are included here, some members of the genus also occur in tropical East Asia and the Himalayas.

The non-monophyly of the pogostemonoids is further corroborated by a general lack of morphological synapomorphies. Although the same lack of morphological synapomorphies applies to the group that also includes three lamioid genera, there are derived morphological traits that corroborate the split of the pogostemonoid labiates into two groups.

Anisomeles and *Pogostemon* both have minute leaf-epidermal glands with unicellular caps, bearded stamen filaments, and a lustrous pericarp (Cantino, 1992a). These two genera also share characters of leaf epidermal anatomy that distinguish them from other labiates (Cantino, 1990). Although no morphological character is found that may serve as a synapomorphy for all four genera, *Craniotome*, *Anisomeles*, and *Pogostemon* all have glossy nutlets (Harley et al., 2004). Furthermore, *Craniotome* and *Pogostemon* both have very small nutlets, a character they share with two monotypic tropical Asian genera, *Colebrookea* Sm. and *Eurysolen* Prain (Harley et al., 2004). The latter two genera are not included in this study (but see below).

There are also morphological characters that suggest a close relationship among the genera of the subclade consisting of the pogostemonoids *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula* and the lamioid *Achyropermum* (Ryding, 1995). The entire clade deviates from the other pogostemonoids as well as most other lamioids in lacking a sclerenchyma

region in the fruit pericarp (Ryding, 1994b, 1995). The shared presence of druses and many cells with pitted to scalariform wall ornamentation in the mesocarp is also a rather uncommon condition.

Even though there are no clear morphological synapomorphies for all genera collectively, we do suggest that this molecularly well-supported group be recognized at the tribal level. The name Pogostemoneae is already available (see Appendix 1). In a phylogenetic analysis of the *trnL-F* region alone, *Eurysolen* grouped in the *Leucosceptrum*–*Rostrinucula*–*Comanthosphace* clade (results not shown). Hence, based on these results, and the strong morphological similarities of *Colebrookea* to this group, these two genera should also be included in Pogostemoneae.

Excluding the three lamioid genera *Achyropermum*, *Craniotome* and *Microtoena*, which group with former Pogostemonoideae as mentioned above, all other members of Lamioideae form a highly supported clade, the Lamioideae s. str. (100% JAC; Fig. 1A).

TRIBE GOMPHOSTEMMATEAE

Within Lamioideae s. str., two temperate East Asian genera, *Bostrychanthera* and *Chelonopsis*, and the tropical East Asian genus *Gomphostemma* form a highly supported clade (95% JAC), which is sister to all other taxa. In contrast to tribe Pogostemoneae, some species of all three of these genera have conspicuously large flowers. Both *Bostrychanthera* and *Gomphostemma* have fleshy fruits and have previously been circumscribed as belonging to the fleshy-fruited tribe Prasieae Benth., whereas *Chelonopsis* was circumscribed as belonging to subtribe Melittidinae Endl. (Bentham, 1848, 1876; Briquet, 1895–1897; see also tribe Synandreae Raf., below). Molecular studies based on both of these suprageneric groups to be polyphyletic (Lindqvist & Albert, 2002; Scheen et al., 2008). The current molecular phylogeny confirms a close relationship between the fleshy-fruited *Gomphostemma* and the dry-fruited *Chelonopsis* as suggested by studies of Lamiaceae fruit pericarp structure (Ryding, 1994c). Furthermore, *Chelonopsis* and *Gomphostemma* deviate from other lamioid labiates by having pollen with branched columellae (Abu-Asab & Cantino, 1994). It is not known whether or not *Bostrychanthera* species share this character. However, the molecular data show that *Chelonopsis* is sister to *Bostrychanthera* rather than being directly sister to *Gomphostemma* (Fig. 1A). Ryding's (1994c) studies showed the pericarp structure of *Chelonopsis* to be particularly similar to that of *G. strobilinum* Wall. and *G. wallichii* Prain, neither of which were included in the current phylogeny. Two morphological characters corroborate the sister relationship of *Bostrychanthera* and *Chelonopsis*: both have

lax inflorescences of long-pedunculate cymes and bearded stamen-filaments (Harley et al., 2004). *Gomphostemma*, on the other hand, has denser and short-pedunculate inflorescences and lacks the bearded stamen-filaments (Harley et al., 2004). Thus, the dry fruit of *Chelonopsis* represents a reversal from a fleshy fruit in the common ancestor to these three genera. Moreover, in *Chelonopsis*, the fruit mesocarp (which is fleshy in *Bostrychanthera* and *Gomphostemma*) deviates by having most of the ordinary tissue replaced by fibers.

Only two species of *Chelonopsis* and one species of *Gomphostemma* and *Bostrychanthera* were included in our analyses. In the future, more species should be investigated to elucidate whether or not *Bostrychanthera* (two spp.), *Chelonopsis* (16 spp.), and *Gomphostemma* (38 spp.) represent monophyletic groups. We recognize these genera as a new tribe Gomphostemmatae Scheen & Lindqvist to reflect the distinct floral traits of the group (see Appendix 1).

GENUS COLQUHOUNIA

The large group of lamioid labiates that is sister to Gomphostemmatae receives moderate resampling support (78% JAC; Fig. 1A). Two (of the ca. six) species of the Asian genus *Colquhounia* Wall. form a moderately supported monophyletic group (77% JAC) that is sister to all remaining taxa. Species of *Colquhounia* have a corolla tube that is strongly dilated in the distal part and nutlets winged at the apex (Harley et al., 2004). The latter character state is rare in Lamioideae. Although *Colquhounia* most likely occupy a phylogenetically distinct position within Lamioideae, we have at this time chosen to leave this clade unclassified at the tribal level.

TRIBE SYNANDREAE

The four North American genera *Brazoria*, *Physostegia*, *Synandra*, and *Warnockia* form a highly supported monophyletic clade (100% JAC; Fig. 1A). A previous study has shown that a fifth North American genus, *Macbridea* Elliott ex Nutt., is a close relative to the other four (Scheen et al., 2008). The monophyly of these five genera is corroborated by a single morphological synapomorphy: a racemose inflorescence with sessile or very shortly pedicellate flowers. All five genera are characterized by having villous stamen filaments (Harley et al., 2004). Although this character may serve as a synapomorphy for the group, it is not entirely unique to the group. Hairs are also present on the stamen filaments of, e.g., *Pogostemon*, *Anisomeles*, and *Chamaesphacos* Schrenk ex Fisch. & C. A. Mey. (Harley et al., 2004). Furthermore, all five genera represent monophyletic

groups that are easily distinguished morphologically (Scheen et al., 2008). The monotypic genus *Synandra* is sister to the other genera and differs from them by having 4-lobed calyces and membranous and long-petiolate leaves that are pubescent on both surfaces, whereas *Brazoria* (two spp.), *Macbridea* (two spp.), *Physostegia* (12 spp.), and the monotypic *Warnockia* have firm-textured, glabrous or almost glabrous, and mostly sessile leaves (Cantino, 1982).

Together with the European genus *Melittis* and the Asian genus *Chelonopsis*, the five North American endemic genera have been circumscribed as subtribe Melittidinae (Benthams, 1848, 1876; Briquet, 1895–1897; see also Cantino, 1985). The current molecular phylogeny shows this group to be unnatural because *Melittis* is the sister taxon to the large *Stachys* clade (see tribe Stachydeae, below; Fig. 1B) and *Chelonopsis* groups within an entirely different Asian clade (see tribe Gomphostemmatae, above; Fig. 1A). The molecular data therefore corroborate the conclusions of several previous studies of morphology, anatomy, and karyology that subtribe Melittidinae should be abandoned (Cantino, 1985; Abu-Asab & Cantino, 1987; Ryding, 1994a). Instead, the five North American endemic genera are circumscribed as tribe Synandreae (Scheen et al., 2008).

The current molecular phylogeny does not show a single genus as sister to the Synandreae. Instead, this group of North American endemics is supported as the sister to the majority of the taxa in Lamioideae s. str., excluding only tribe Gomphostemmatae and the genus *Colquhounia* (Fig. 1A). Although members of Gomphostemmatae and *Colquhounia* are East Asian, it is not possible to conclude how Synandreae arrived in North America, whether via a transatlantic or transpacific migration. However, our results do demonstrate that the Synandreae represent a single migration into North America that is separate from that of the *Stachys* clade (see tribe Stachydeae, below). Thus, there have been at least two separate invasions of North America by lamioid labiates. The evolutionary histories of Synandreae and the *Stachys* clade differ greatly after their establishment in North America. The *Stachys* clade radiated into a morphologically and ecologically diverse group that spread farther into South America and the Hawaiian archipelago (Lindqvist & Albert, 2002). The Hawaiian labiates alone comprise ca. 59 species and show a remarkable morphological and ecological variation, albeit with low levels of DNA sequence variation (Lindqvist et al., 2003). The 19 species of Synandreae do not show a similar radiation. Most of the taxa have restricted distributions and four of the five genera comprise three or fewer species (Harley et al., 2004). The exception is the more species-rich genus

Physostegia. Although many of the 12 species have restricted distributions, the genus is widespread in North America (Cantino, 1982). *Physostegia* does occur in a great diversity of habitats and appears to tolerate a broad range of soil acidity (Cantino, 1982); however, the morphological variation within the genus is low and can best be described as kaleidoscopic (Cantino, 1982). The low level of morphological variation is mirrored by low levels of DNA sequence variation (Scheen et al., 2008).

The large sister clade of the *Synandreae* receives moderate resampling support (82% JAC; Fig. 1A). The majority of the genera in this clade are distinguished from the rest of *Lamioideae* in having fruit exocarp strongly differentiated into two types of cells, a thin-walled and a thick-walled type (Ryding, 1995). However, the exocarp differentiation character is very homoplastic. Ryding (1995) has also recorded a weak and vague differentiation of the cells in the exocarp of *Microtoena*, which lies well outside this clade in *Pogostemoneae* (Fig. 1A), but in this genus, the slightly thick-walled cells diverge in being arranged in large groups.

GENERA *BETONICA* AND *GALEOPSIS*

All included representatives of *Stachys* subg. *Betonica* form a strongly supported clade separate from all remaining members of *Stachys* (100% JAC; Fig. 1B). The five included species, and about 10 other *Stachys* species distributed in western Eurasia, are morphologically distinct from the remainder of *Stachys* and have at various times been assigned to a separate genus *Betonica* L. (e.g., Dumortier, 1827; Bentham, 1829; Reichenbach, 1830–1832; Cosson & German, 1845). Morphologically, *Betonica* is readily distinguished from the remainder of *Stachys* by having a persistent rosette of leaves, flowering stems lateral to rootstock, sessile flowers, flowers and bracteoles with a broad and hardened base, and anther cells that are parallel (Ball, 1972; Bhattacharjee, 1980). Also, phytochemistry supports the distinction between *Betonica* and remaining *Stachys* species (Tomas-Barberan et al., 1992). An ostensibly great pollen similarity reported between *Betonica* and *Stachys* (Krestovskaya & Vasileva, 1997) was likely due to limited taxon sampling; no other lamioid genera were included. As previously suggested (Lindqvist & Albert, 2002), our results clearly corroborate that the genus *Betonica* L. should be reestablished.

Within the *Betonica* clade, no clear distinction between the two sections *Betonica* (L.) Benth. and *Macrostachya* R. Bhattacharjee is apparent from our molecular data. *Betonica alopecuroides* L., however, is sister to the remaining four species (Fig. 1B). This

species is morphologically distinct with yellow flowers with a bifid upper corolla lip, and an annulate corolla tube (Ball, 1972; Bhattacharjee, 1980).

Our results strongly support monophyly of *Galeopsis* (100% JAC; Fig. 1B). *Galeopsis* comprises 11 annual species, all with their center of diversity in Europe. There are two clear morphological synapomorphies for this genus: the presence of two conical protuberances near the base of the anterior lip of the corolla, and anthers dehiscing by two valves, of which the upper is fimbriate (Townsend, 1972; Harley et al., 2004). A comprehensive phylogenetic study of *Galeopsis* will be published elsewhere (Bendiksby et al., unpubl.).

Both the clade comprising *Betonica* and *Galeopsis*, as well as its sister relationship to tribe *Stachydeae*, is not supported with resampling and is retained only in the strict consensus of the indel-coded analysis (Fig. 1B). It should be noted, however, that *Betonica* and *Galeopsis* share the same basal chromosome number ($x = 8$; Goldblatt & Johnson, 2006), and that flavonoid p-coumaroyl glucosides are present in both *Betonica* and subgenus *Galeopsis* (Tomas-Barberan et al., 1992). Nevertheless, it was an unexpected result that *Galeopsis* should be more closely related to *Betonica* than to *Lamium* and *Lamiastrum*, with which it has been classified in most traditional classifications; e.g., *Galeopsis*, *Lamium*, and *Lamiastrum* were classified as subtribe *Galeopsidinae* Dumort. based on the shared feature of a swollen corolla tube (Dumortier, 1827). Because of the uncertain positions of these two genera in our current molecular phylogeny, and in order to avoid phylogenetic redundancy, we have chosen to leave the genera unclassified at the tribal level here.

TRIBE STACHYDEAE

The monotypic genus *Melilotis*, distributed in eastern Europe and western Asia, is strongly supported as sister to the *Stachys* s.l. clade (100% JAC; Fig. 1B). We have chosen to recognize this greater clade as tribe *Stachydeae* (see Appendix 1). It should be noted, however, that the perennial herb, *Melilotis melissophyllum* L., is clearly distinct from the *Stachys* s.l. clade, characterized by very large flowers and a 2-lipped calyx, with the upper lip entire or irregularly dentate (Harley et al., 2004).

Stachys, as currently circumscribed, comprises approximately 300 species (Harley et al., 2004). It is the largest genus of subfamily *Lamioideae* and among the largest genera of the entire *Lamiaceae*. Results from our molecular phylogenetic analysis confirm that the subcosmopolitan genus *Stachys* represents an unnatural group in strong need of revision (Lindqvist & Albert, 2002; Fig. 1B). Lindqvist and Albert (2002) have previously shown that

the lamioid genera *Sideritis*, *Prasium* L., *Phlomidioschema* Vved., and the Hawaiian endemic labiates (*Haplostachys* (A. Gray) Hillebr., *Phyllostegia* Benth., and *Stenogyne* Benth.) are nested within *Stachys* s.l. Our present results, which include a more extensive sampling of mostly Old World species, corroborate these findings and demonstrate that the Asian genera *Chamaesphacos*, *Suzukia* Kudô, and *Thuspeinanta* T. Durand are also embedded within *Stachys* s.l. (Fig. 1B), relationships that have not been previously suggested. Our molecular data subdivide the large *Stachys* s.l. clade into two strongly supported clades, both including *Stachys* as well as non-*Stachys* genera (Fig. 1B): clade A (99% JAC) comprises the Hawaiian endemics, temperate East Asian *Suzukia*, and largely New World *Stachys* species, including the North American *Stachys*, as well as a clade of sub-Saharan African species, and clade B (100% JAC) includes the genera *Sideritis*, *Prasium*, *Phlomidioschema*, *Thuspeinanta*, *Chamaesphacos*, and Old World *Stachys* species.

The many small genera embedded within tribe Stachydeae vary in their degree of morphological distinctness. The genus *Suzukia* includes two species of creeping perennial herbs that are endemic to forests of Taiwan and the Ryukyu Islands (Harley et al., 2004). Monophyly of *Suzukia* is only weakly supported by our cpDNA phylogeny (62% JAC; Fig. 1B, clade A), and the genus may be difficult to distinguish morphologically from related taxa. An orbicular leaf blade, a moderately long posterior corolla lip (Harley et al., 2004), and a haploid chromosome number of $n = 17$ (Goldblatt & Johnson, 2006) may represent synapomorphic characters for the genus.

Haplostachys (five spp.), *Phyllostegia* (ca. 34 spp.), and *Stenogyne* (ca. 20 spp.) have been classified together with *Prasium*, *Bostrychanthera*, and *Gomphostemma* as tribe Prasieae (Bentham, 1848) or as subfamily Prasioideae (Briquet, 1895–1897) because of the fleshy fruits borne by these genera (except *Haplostachys*). Although the Hawaiian labiates and the Mediterranean monotypic *Prasium* belong in the *Stachys* s.l. clade, they group in separate clades (A and B, respectively; Fig. 1B), and it is clear that fleshy fruits represent a homoplastic trait within Lamiodeae (see also Issues in Lamioid Character Evolution, below). *Prasium majus* L., a small, usually glabrous shrub, is resolved as sister to a clade comprising species of *Stachys*, *Sideritis*, *Phlomidioschema*, *Thuspeinanta*, and *Chamaesphacos* (Fig. 1B, clade B). The western to central Asian *Phlomidioschema* attains a more derived position in this clade and is discriminated by a woody base, a dense cover of branched hairs, entire leaf margins, calyx strongly accrescent in fruit, and few-flowered cymes. The

perennial monotypic *Phlomidioschema* and two species of *Stachys* form a polytomy that also includes a strongly supported clade comprising the two western Asian genera *Chamaesphacos* and *Thuspeinanta* (100% JAC; Fig. 1B). Both *Chamaesphacos* and *Thuspeinanta* are annuals bearing very narrow nutlets and short stamens. The monotypic *Chamaesphacos* is characterized by spiny leaf margins, a long corolla tube with a short and flat upper lip and anterior lip deflexed, and membranous-winged nutlets (Harley et al., 2004). *Chamaesphacos* has previously been associated with *Craniotome*, *Anisomeles*, *Achyrosperrum*, and *Colquhounia* based on the shared presence of a short, flat, and glabrous upper corolla lip (Bentham, 1876). The two species of *Thuspeinanta* are characterized by being annual and having bracteoles that recurve in fruit, calyx lobes that are inflated in fruit, and confluent anther-thecae (Harley et al., 2004). *Thuspeinanta* has previously been classified with *Acrotome*, *Marrubium*, and *Sideritis* as tribe Marrubieae Vis. (Bentham, 1876; Briquet, 1895–1897). In our molecular phylogeny, *Thuspeinanta* is paraphyletic with respect to *Chamaesphacos* and may hold a derived position within clade B of the *Stachys* s.l. clade (Fig. 1B).

All included members of *Sideritis* are confined to clade B (Fig. 1B). Both *Sideritis* and *Stachys* are large non-monophyletic genera within subfamily Lamiodeae (Fig. 1B), and both show an extensive morphological, karyotypic, and ecological diversity that overlap (Harley et al., 2004). *Sideritis* (ca. 140 spp.), which is found from Macaronesia to western China with a circum-Mediterranean center of distribution, is characterized by having verticillasters in terminal spikes, corolla tube shorter than calyx, posterior corolla lip almost flat, and confluent anther thecae (the latter feature is also seen in *Thuspeinanta*; Harley et al., 2004). In their study of the origin of Macaronesian *Sideritis*, Barber et al. (2002) assumed the genus *Sideritis* to be monophyletic, but following Lindqvist and Albert (2002), we show here that *Sideritis* as currently circumscribed is paraphyletic, and that phylogenetic relationships of *Sideritis* are complex. Furthermore, none of the sectional subdivisions of *Sideritis* (Briquet, 1891–1895) or *Stachys* (Bhattacharjee, 1980) are monophyletic in our phylogenetic analyses (Fig. 1B).

We found no non-molecular features that could characterize all members of tribe Stachydeae: stamens included in the corolla tube. However, this feature does not distinguish tribe Stachydeae from most other lamioid groupings (see Issues in Lamioid Character Evolution—Stamen Length, below). However, there are a few morphological features that characterize the majority of Stachydeae. These include: calyx often

campanulate or weakly 2-lipped with lobes often spiny and throat often hairy, and corolla often strongly 2-lipped. This morphologically and ecologically diverse assemblage, comprising at least 11 genera, clearly needs further investigation.

GENUS *PARAPHLOMIS*

The remainder of Lamiioideae constitutes a monophyletic group (94% JAC; Fig. 1C) comprising some well-supported genera. However, many genera are intercalated within one another, perhaps confused taxonomically by homoplastic morphological traits (as mirrored, e.g., in Stachydeae by *Stachys* and *Sideritis*). The condition of having the nutlets apically truncate may constitute a synapomorphy of this group, but there are reversals to apically rounded nutlets within *Paraphlomis* and all of the following tribes. The genus *Paraphlomis* (Prain) Prain together with the *Phlomis* clade form a trichotomy with respect to all remaining taxa (Fig. 1C). *Paraphlomis*, as currently circumscribed, includes about 20 species that occur mostly in forests and on hill slopes in tropical and subtropical East Asia. *Paraphlomis* has previously been reduced to a section within *Phlomis*, including the three species *Paraphlomis rugosa* (Benth.) Prain, *P. oblongifolia* (Blume) Prain, and *P. javanica* (Blume) Prain (Prain, 1901). Although our analyses do place two accessions of *Paraphlomis* in the vicinity of *Phlomis*, the phylogenetic position of *Paraphlomis* is still uncertain and no higher-level classification is suggested at this time.

TRIBE PHLOMIDEAE

Phlomis comprises more than 100 species distributed throughout western Eurasia. Infrageneric relationships of *Phlomis* were recently investigated using the *trnL-F* region and *rps16* intron (Mathiesen, 2006; Mathiesen et al., unpubl.). Despite considerable morphological and ecological variation among taxa, sequence variation was found to be remarkably low, resulting in poor phylogenetic resolution, especially among the southwestern Asian and Mediterranean species. However, the results supported a split of the genus into two separate groups, which can be recognized as separate genera. Our findings here, based on a more limited sampling of *Phlomis* species, corroborate a split of the genus into two species groups: *Phlomis* s. str. and *Phlomoideis* Moench s.l. (clades C and D, respectively, Fig. 1C). *Phlomoideis*, the non-type group, includes the west Eurasian genus *Eremostachys* (five to 60 spp.), the small subtropical to tropical East Asian genus *Notochaete* (two spp.), and the monotypic West Asian genus *Pseudermostachys* (clade D, Fig. 1C). The division of *Phlomis*

species into two groups is supported by several traits, including habit, leaf characters, corolla morphology, cytological data (Azizian & Cutler, 1982; Azizian & Moore, 1982), and pericarp structure (Ryding, 2008), and it has recently been suggested that the two groups of *Phlomis* species be raised to the generic level (Adylov et al., 1986; Kamelin & Makhmedov, 1990a, b; Ryding, 2008). Moreover, two centers of diversity can be recognized: (1) south and east Anatolia and northwestern Iran, where all but one species belong to the *Phlomis* group, and (2) Central Asian parts of the former USSR to eastern parts of China, where all species of the *Phlomoideis* group occur (Azizian & Moore, 1982).

A close relationship between *Phlomis* and *Eremostachys* has previously been suggested. Consequently, several species of *Eremostachys* were transferred to *Phlomoideis*, including the only species of *Eremostachys* in the current phylogeny, while other species were transferred to *Paraeremostachys* Adylov, Kamelin & Makhm. (Adylov et al., 1986; Kamelin & Makhmedov, 1990a, b). However, as mentioned by Hedge (1990), the name *Paraeremostachys* is illegitimate; the type of this name is also the type of *Eremostachys*. Both *Phlomoideis* and *Paraeremostachys* are treated as synonyms by Harley et al. (2004). Until molecular data are available for more species of *Eremostachys*, no nomenclatural changes are proposed. However, we still recognize these genera as part of the *Phlomis* group and classify this clade as tribe Phlomoideae Mathiesen (see Appendix 1). Although not included here, based on strong morphological similarities and phylogenetic analyses based on cpDNA data (Mathiesen et al., unpubl.), the monotypic genus *Lamiophlomis* Kudô should also be included in this tribe.

TRIBE LEONUREAE

The four temperate Eurasian genera *Chaiturus*, *Lagochilus*, *Leonurus*, and *Panzerina* group with high support (95% JAC; Fig. 1C) and are moderately supported as sister to a large polytomy consisting of all remaining taxa. Based on these results, we suggest that *Chaiturus*, *Lagochilus*, *Leonurus*, and *Panzerina* be classified as tribe Leonureae Dumort. (see Appendix 1). Furthermore, in a phylogenetic analysis of the *trnL-F* region alone (results not shown), the small genus *Lagopsis* (Bunge ex Benth.) Bunge groups within the *Chaiturus*-*Leonurus*-*Panzerina* clade and should also be included in Leonureae. Short stamens that are included in the corolla tube, palmate leaf venation, and often palmately lobed leaves may be synapomorphies for the group. Although *Leonurus*, *Chaiturus*, and *Panzerina* have been associated in traditional classifications, their close relationship to *Lagochilus* and *Lagopsis* has not previously been suggested. *Lagopsis*

was classified in a separate tribe from that of the other four genera by Takhtajan (1997), and Mabberley (1997) regarded *Lagopsis* as synonym to *Marrubium*.

A monophyletic and strongly supported (100% JAC) *Lagochilus* is recovered as sister to a clade including the remaining four genera (Fig. 1C). Morphologically, *Lagochilus* (ca. 40 spp.) is the most distinct genus of the four, with spiny bracteoles longer than calyces, spines usually present in the leaf axils, and a densely villous, 2-lobed, long and narrow posterior corolla lip (Harley et al., 2004). Three small genera, *Lagopsis* (four spp.), *Panzerina* (two to seven spp.), and the monotypic *Chaiturus*, are nested within a paraphyletic *Leonurus* (ca. 25 spp.). These four genera group in all trees and differ from *Lagochilus* in having shorter bracteoles, no spines in leaf axils, and a short posterior lip of the corolla (Harley et al., 2004).

Chaiturus and *Panzerina* have been variously associated with *Leonurus* in traditional classifications (Dumortier, 1827; Reichenbach, 1830–1832; Endlicher, 1836–1840; Bentham, 1876; Briquet, 1895–1897; Wu & Li, 1982; Harley et al., 2004). Included or excluded, *Chaiturus* and *Panzerina* have always been recognized as divergent in several features from *Leonurus* s. str. and classified separately at some level. *Chaiturus* differs from *Leonurus* in the structure of the calyx, the arrangement of stamens, leaf shape, and chromosome number (Harley et al., 2004). *Panzerina* differs from *Leonurus* in the size, color, and shape of the corolla and the surface morphology of nutlets (Harley et al., 2004). *Chaiturus* and *Panzerina* also differ from *Leonurus* ecologically and biogeographically. *Chaiturus marrubiastrum* (L.) Spenn. is a ruderal species in the European-Mediterranean region, whereas the *Panzerina* species are endemic to semi-deserts of Central Asia (Harley et al., 2004). *Lagopsis*, which is widely distributed throughout temperate Asia, differs morphologically from *Leonurus* in corolla and nutlet morphology, and by being densely white-lanate (Harley et al., 2004).

Based on the paraphyly of *Leonurus*, as well as the morphological and karyotypic discontinuity within the group, we suspect that *Leonurus* may have been originally established based on plesiomorphic characters. More species should be added prior to a more thorough evaluation of generic status of groups within this clade.

A LARGE POLYTOMY

Sister to tribe Leonureae is a weakly supported clade consisting of all remaining taxa (58% JAC; Fig. 1C). This clade is native to Old World temperate, subtropical, or tropical areas, although a few species have been introduced elsewhere (e.g., the widespread *Marrubium vulgare* L. and *Leonotis nepetifolia* (L.) R.

Br.). This large group of taxa is separated into three groups and the monotypic genus *Roylea* Wall. ex Benth., which together form a polytomy (Fig. 1C). *Roylea*, and the likewise monotypic *Eriophyton* Benth., occur at high altitudes in the Himalayas. Tribes Lamieae Coss. & Germ., Marrubieae, and Leucadeae Scheen & Ryding all include species from temperate western Eurasia with extensions into subtropical to tropical zones. Given their uncertain phylogenetic placements in our analyses, we have not classified *Roylea* and *Eriophyton* at the tribal level.

TRIBE LAMIEAE

Our results strongly support a clade comprising the three genera *Lamium* (ca. 35 spp.), *Lamiastrum* (one to four spp.), and *Wiedemannia* (two spp.) (99% JAC; Fig. 1C), which we have chosen to classify as tribe Lamieae (see Appendix 1). Lamieae has a temperate Eurasian distribution with center of diversity in western Asia (the Irano-Turanian region; Mennema, 1989). Synapomorphies of the group include hairy anthers, an abruptly widening corolla tube, and often pubescent corollas with a long and hooded upper lip. A close *Lamium*–*Lamiastrum* relationship has been suggested in most traditional classifications and was therefore expected. The two annual *Wiedemannia* species have also been taxonomically associated with *Lamium* (Endlicher, 1836–1840; Bentham, 1876). While most authors agree on a close relationship between *Lamium*, *Lamiastrum*, and *Wiedemannia*, classifications have varied as to the autonomy of the latter two genera (see, e.g., Dumortier, 1827; Reichenbach, 1830–1832; Endlicher, 1836–1840; Cosson & German, 1845; Bentham, 1876; Luerssen, 1879–1882; Krause, 1903; Mennema, 1989; Ryding, 2003; Harley et al., 2004). The separation of *Lamiastrum* has been based on differences in the shape and color of the corolla, whereas *Wiedemannia* is characterized by a 2-lipped calyx (Harley et al., 2004). In the most recent treatment of Lamiaceae (Harley et al., 2004), both *Lamiastrum* and *Wiedemannia* are treated as synonyms of *Lamium*, although it is also stated that the very distinct *Lamiastrum* may be better treated as a separate genus, and that most authors treat *Wiedemannia* as a separate genus. The monotypic Himalayan *Eriophyton*, which agrees with most *Lamium* in having hairy anthers, is sister to tribe Lamieae in all analyses. However, this relationship is poorly supported (56% JAC; Fig. 1C). Other Asian lamioide genera that could not be examined here, but nevertheless might be relevant to Lamieae phylogeny include *Ajugoides* Makino, *Matsumurella* Makino, *Loxocalyx* Hemsl., and *Alajia* Ikonn. A comprehensive

phylogenetic study of the group will be published elsewhere (Bendiksby et al., unpubl.).

TRIBE MARRUBIEAE

Species of *Ballota*, *Marrubium*, and *Moluccella* form a well-supported monophyletic group (84% JAC; Fig. 1C). *Ballota integrifolia* Benth., which is endemic to Cyprus, is sister to all other taxa. Together with the European species *B. frutescens* (L.) Woods, *B. integrifolia* has been circumscribed as belonging to section *Acanthoprasium* Benth. (Patzak, 1959). The key characters for section *Acanthoprasium* are woody habit and the presence of long and spinose bracteoles (Patzak, 1959; Harley et al., 2004). All other species of *Ballota* are herbs or subshrubs with herbaceous bracteoles. It may be that *B. integrifolia* deserves to be recognized as a separate genus based on its molecular and morphological distinctness from the other *Ballota* species; however, *B. frutescens* could not be included in the current phylogeny and therefore no taxonomic changes are suggested at this time.

The three species of *Moluccella* form a highly supported group (99% JAC; Fig. 1C). *Moluccella* is found in rocky and disturbed regions from southern Europe to central Asia. *Moluccella aucheri* (Boiss.) Scheen was recently transferred from *Otostegia* to *Moluccella* based on molecular data and morphological characters (Scheen & Albert, 2007, 2009). The monotypic genus *Sulaimania* Hedge & Rech. f. was separated from *Moluccella* based on its perennial and subshrubby habit, unexpanded fruiting calyx limb, and different overall appearance (Hedge & Rechinger, 1982). Unfortunately, *Sulaimania*, which is endemic to dry places in western Pakistan, could not be included in the current phylogeny. The unexpanded calyx limb is anomalous in *Moluccella*; however, *Sulaimania* is said to superficially resemble *M. aucheri* (Hedge & Lamond, 1968; Hedge & Rechinger, 1982). In the original circumscription of the species (as *M. otostegioides* Prain), Prain (1890) describes it as having the habit of *M. aucheri* with a calyx like that of *M. spinosa* L., only smaller. Further studies are needed to verify the monotypic status of *Sulaimania* and the nature of its relationship to *Moluccella* and other genera of Lamiaceae. Regardless, *Moluccella* forms a well-supported monophyletic group (99% JAC) that is sister to a well-supported group (100% JAC) consisting of *Marrubium* and *Ballota* (Fig. 1C).

Most species of *Ballota* form a well-supported clade with *Marrubium* (100% JAC; Fig. 1C), thus confirming a close relationship between these two genera. The *Ballota* and *Marrubium* species with branched hairs on the vegetative parts form a large subclade (66% JAC; Fig. 1C) with *B. nigra* L. as sister. The only character

used to distinguish members of the two genera is the position of the stamens, i.e., whether stamens are included in the corolla tube as in *Marrubium* or shortly exserted from the corolla as in *Ballota* (Harley et al., 2004). The genus *Ballota* includes about 30 species distributed in Eurasia and North Africa, with one species (*B. africana* (L.) Benth.) being endemic to South Africa and Namibia. The current molecular phylogeny clearly demonstrates that the genus *Ballota* as currently circumscribed does not represent a monophyletic group. However, the five species of *Ballota* that form a well-supported subclade (99% JAC; Fig. 1C) are all members of the large section *Beringeria* (Neck.) Benth. sensu Briquet (1895–1897). The genus *Marrubium* includes approximately 40 species that are distributed from Europe through Pakistan to the Himalayas and in North Africa, mainly in rather dry places. Based on the current molecular phylogeny, it is not possible to say whether or not *Marrubium* is monophyletic as currently circumscribed. Three of the included species form a strongly supported group (100% JAC; Fig. 1C), whereas the fourth species is unresolved with respect to *Ballota*. Although the status of *Marrubium* and *Ballota* remains unresolved, the name Marrubieae is already available to encompass the entire clade, i.e., *Ballota*, *Marrubium*, and *Moluccella* (see Appendix 1).

TRIBE LEUCADEAE

As part of the large polytomy, species of the six genera *Acrotome*, *Isoleucas*, *Leonotis*, *Leucas*, *Otostegia*, and *Rydingia* form a well-supported group recognized here as tribe Leucadeae (100% JAC; Fig. 1C; see Appendix 1). Based on a phylogenetic analysis of many more representatives of Leucadeae, several taxonomic changes have recently been suggested (Scheen & Albert, 2007, 2009).

The genus *Otostegia* was recently reclassified and the number of species was reduced from 17 to 11, all with an African to Arabian distribution occurring in dry, often montane areas and semideserts (Scheen & Albert, 2007, 2009). Species of *Otostegia* lack spines at the leaf axils and have herbaceous bracteoles and white flowers (Sebald, 1973; Rechinger, 1982; Ryding, 1998; Scheen & Albert, 2007, 2009). Of the excluded six species, one species was transferred to *Isoleucas* (*I. somala* (Patzak) Scheen) based on molecular data as well as a few morphological characters including minute bracteoles, small, almost round leaves, a 5-lobed calyx, and most parts of the plants being densely white tomentose (Sebald, 1973; Scheen & Albert, 2007). Another species was transferred to *Moluccella* (*M. aucheri*; see tribe Marrubieae, above). Finally, four species were transferred to the new genus *Rydingia* (Scheen & Albert, 2007, 2009). *Rydingia* differs from

the remaining species of *Otostegia* in having spines at the leaf axils, spinose and persistent bracteoles, yellow flowers, and few-flowered verticillasters (Sebald, 1973; Rechinger, 1982; Ryding, 1998). With the recircumscriptions of *Isoleucas* and *Otostegia* and the recognition of *Rydingia*, all three genera are well-supported monophyletic groups (Fig. 1C). However, although *Rydingia* is highly supported (100% JAC) as sister to all other species of the *Leucas* s.l. clade, *Otostegia* and *Isoleucas* are nested within *Leucas* (Fig. 1C).

The genus *Leucas* is one of the largest genera of subfamily Lamioideae with about 100 species occurring on dry or disturbed ground in tropical to southern Africa and tropical and subtropical parts of Asia (Harley et al., 2004). Most species are restricted to either Africa (including the Arabian Peninsula) or Asia (excluding the Arabian Peninsula), although a few species are more widely distributed (e.g., *L. aspera* (Willd.) Link and *L. martinicensis* (Jacq.) R. Br.; Singh, 2001). Asian and African species of *Leucas* form separate groups with the primarily Asian species being supported as a monophyletic group (88% JAC), whereas the African species are not (Fig. 1C; Scheen & Albert, 2009). The African species of *Leucas* are paraphyletic with respect to the African genera *Acrotome* and *Leonotis*, as well as the African species of *Otostegia*. The molecular data corroborate the results of a previous morphologically based phylogeny, but whereas *Acrotome* and *Leonotis* form monophyletic groups based on the morphological data (Ryding, 1998), they do not form monophyletic groups based on molecular data (Fig. 1C; Scheen & Albert, 2009).

The nine species of *Leonotis* occur on hilly slopes and rocky or disturbed ground in tropical and southern Africa and are easily recognized by the bright orange or red corollas of their flowers and the short lower corolla lip that withers at anthesis (Ryding, 1998; Iwarsson & Harvey, 2003). The six species of *Acrotome* occur in dry places in south tropical and southern Africa (Harley et al., 2004). *Acrotome* is separated from *Leucas* and *Leonotis* based on short stamens that are included in the corolla tube, a hairy style, and the lack of a bearded margin of the posterior corolla lip (Ryding, 1998; Harley et al., 2004). The non-monophyly of *Leonotis* seems particularly strange given the suite of characters (related to bird pollination) shared by all members of the genus. Preliminarily, we suggest that cpDNA capture via hybridization could account for the relationships seen between particular species of *Leonotis* and *Leucas*.

ISSUES IN LAMIOID CHARACTER EVOLUTION

With the extensive sampling across subfamily Lamioideae and the resulting molecular phylogeny, it

is possible to suggest some patterns of character evolution within the subfamily. A few monotypic or small genera could not be included in this study, and some of the large genera are only represented by one or two species. Therefore, the current results do not paint a complete picture. Despite these limitations, it is clear that several morphological characters that were treated by previous system-builders as good diagnostic characters for specific groups (e.g., Bentham, 1876) are not synapomorphies exclusive to these groups but have evolved several times. Most genera of Lamioideae have thyrsoid inflorescences, but tribe Synandreae has racemoid inflorescences, and in some groups both types of inflorescence occur, e.g., in tribe Stachydeae, *Ballota*, and *Marrubium* (Harley et al., 2004). Lamioid labiates vary in habit from annual herbs to subshrubs, shrubs, and rarely even small trees (Harley et al., 2004). Woodiness has evolved repeatedly from herbaceous ancestors in several asterid groups, e.g., in Apiaceae subfam. Apioideae (Calviño et al., 2006) and in the family Gentianaceae (Struwe & Albert, 2002). In subfamily Lamioideae, the reverse has also occurred: the herbaceous habit, e.g., in *Comanthosphaea* (Pogostemoneae), has clearly evolved from woody ancestors. Many lamioid genera (e.g., *Leucas*, *Phlomis*, and *Pogostemon*) include both herbs and shrubs or subshrubs, suggesting that overall habit in Lamioideae is a highly homoplastic trait. In a few genera, the calyx is expanded into a dilated limb, e.g., *Moluccella* and *Otostegia*, and in a few genera the calyx is strongly accrescent in fruit, e.g., *Colebrookea*, *Paralamium* Dunn, and *Phlomidioschema* (Harley et al., 2004). Indeed, several striking patterns of parallelism emerge from the current phylogeny, as discussed separately and in more detail for some other characters in the following sections.

Fleshy fruits. A well-known case of parallelism within lamioid labiates is the development of a fleshy fruit. Because most labiates have dry fruits, it was once thought that fleshy fruits had evolved only once, and genera with fleshy fruits were circumscribed as tribe Prasieae (Bentham, 1848) or as subfamily Prasioideae (Briquet, 1895–1897). However, recent studies of fruit pericarp structure and molecular relationships of lamioid labiates have shown that fleshy fruit is a homoplastic trait (Ryding, 1994c; Lindqvist & Albert, 2002). A fleshy fruit has developed at least three times among lamioid labiates: among the Hawaiian labiates (*Stenogyne* and *Phyllostegia*), in *Prasium*, and in two genera of the Gomphostemmaeae (*Gomphostemma* and *Bostrychanthera*). Not only have there been three independent origins of fleshy fruit, but the current molecular phylogeny also suggests there has been at least one

reversal from a fleshy fruit in the common ancestor of *Bostrychanthera*, *Chelonopsis*, and *Gomphostemma* to a dry fruit in the genus *Chelonopsis*. In monocots, fleshy fruits have evolved and been lost repeatedly, and a strong tendency for fleshy fruits to evolve in the shade and be lost in open habitats has been demonstrated (Givnish et al., 2005). In Lamioideae, a shady habit does not seem to be linked to presence of a fleshy fruit. Fleshy-fruited *Prasium*, for example, occurs in dry, open places (Harley et al., 2004). Many other examples of parallel evolution of fleshy fruits from dry-fruited ancestors exist, e.g., in Rosaceae (Potter et al., 2007), Rubiaceae (Bremer & Eriksson, 1992; Rova et al., 2002), and Solanaceae (Knapp, 2002).

Stamen length. Having short stamens that are included in the corolla tube, rather than exserted, is a character that has been used historically to distinguish several genera: *Marrubium* from *Ballota*, *Acrotome* from *Leucas* and *Leonotis*, and *Sideritis* from *Stachys*. The shared presence of short stamens led Bentham and Briquet to place *Marrubium*, *Acrotome*, and *Thuspeinanta* in tribe Marrubieae (Bentham, 1876; Briquet, 1895–1897), although this view has not been supported by later authors (e.g., Sebald, 1980; Ryding, 1998).

Most genera of Lamioideae are described as having stamens that are not or only shortly exserted from the corolla (Harley et al., 2004). However, a few genera have stamens that are long and clearly exserted from the corolla. This trait may be considered a synapomorphy for the clade consisting of *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula*, but it is also found in *Pogostemon* (Harley et al., 2004; see Pogostemoneae, above). Thus, long-exserted stamens have evolved at least twice within the lamioideae but are restricted to tribe Pogostemoneae (Fig. 1A). The differences in stamen position and length are most likely related to differences in pollination syndrome.

Indumentum. Many labiates have densely hairy corollas, most often on the outside as in *Lamium*, *Moluccella*, *Leucas*, and *Phlomis*, but also sometimes on the inside of the corolla as in *Lagochilus* (Harley et al., 2004). Although it is easy to distinguish between a glabrous and a densely hairy floral part, it is more difficult to quantify the degree of indumentum between the two extremes. Even so, type and amount of indumentum often vary enough to be used in keys. The presence versus absence of branched hairs was used in the key to subfamily Lamioideae (Harley et al., 2004) and also to distinguish the monotypic genus *Isoleucas* (Schwartz, 1939). However, with the recent transfer of *Otostegia somala* (Patzak) Sebald to *Isoleucas*, presence of branched hairs is no longer a diagnostic character for the genus (Scheen & Albert,

2007, 2009). Although presence of branched hairs is sometimes shared among closely related taxa, e.g., *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula*, it is a character that has evolved several times within subfamily Lamioideae, e.g., in *Ballota*, *Gomphostemma*, *Isoleucas*, and *Pogostemon*.

Several genera of subfamily Lamioideae are characterized by having a bearded margin of the posterior corolla lip, but this feature is only found in Phlomideae and Leucadeae. In the genus *Phlomis*, the presence versus absence of a bearded corolla margin supports the segregation of the *Phlomoides* s.l. (including *Notochaete* and at least some of *Eremostachys*) from *Phlomis* s. str. (Mathiesen, 2006; see tribe Phlomideae, above). In tribe Leucadeae, the bearded corolla margin is present in all genera except the derived genus *Acrotome*. Thus, it appears there has been a reversal of the trait in the lineage leading to *Acrotome* (Scheen & Albert, 2009). The lack of the characteristic bearded corolla margin was one of the morphological characters supporting the transfer of *Otostegia aucheri* Boiss. to *Moluccella* and thereby the segregation from *Otostegia* (Scheen & Albert, 2007). Whether or not different indumentum characters represent phylogenetically informative characters seems to vary widely between clades and characters. However, presence of a bearded margin of the posterior corolla lip may be an example of a phylogenetically informative character that may be taken as a synapomorphy for two different groups. It seems to have evolved twice with at least one reversal of the trait (Fig. 1C).

Spinose bracteoles. Most genera of subfamily Lamioideae have herbaceous bracteoles, but a few genera are characterized by having spinose or spinescent bracteoles, e.g., *Galeopsis*, *Lagochilus*, *Leonotis*, and *Moluccella* (Harley et al., 2004; Fig. 1B, C). Based on the relationships uncovered in the current phylogeny, this is another trait that has evolved several times independently. Furthermore, this character can be continuous, and distinguishing between mucronate, apiculate, spinescent, and spinose bracteoles can be difficult, e.g., in *Leonotis*, where intermediate states are common. Nevertheless, the presence of spinose bracteoles does seem to hold a phylogenetic signal at the generic level. In several cases, species with spinose bracteoles do not group with their congeners with herbaceous bracteoles. The presence of spinose bracteoles is one of the morphological characters that support the transfer of *Otostegia aucheri* to *Moluccella* and the segregation of the newly described genus *Rydingia* from *Otostegia* (Scheen & Albert, 2007, 2009; see Fig. 1C and tribe Leucadeae, above). Also, in *Ballota*, presence versus absence of spinose bracteoles coincides with the molecular relationships uncovered in the current

phylogeny and may warrant the segregation of *B. integrifolia* and *B. frutescens* from the remaining species of *Ballota* (see Fig. 1C and tribe Marrubieae, above). In all of these cases, presence of spinose bracteoles is corroborated by other morphological characters that support the generic segregations.

Calyx fibers. Ryding (2007) studied the amount of fibers in calyces of Lamiaceae and found particularly high quantities in the subfamilies Lamioideae and Scutellarioideae. Although the character is very homoplastic, it is interesting to note that the variation in amount of calyx fibers appears to be rather strongly correlated to the topology of the current cladistic hypothesis (Fig. 1). The amount of fibers is generally very high in the large clade of *Paraphlomis*, *Phlomis*, *Leonurea*, *Lamieae*, *Marrubieae*, and *Leucadeae* (Fig. 1C); generally intermediate in the clade of *Betonica*, *Galeopsis*, and *Stachydeae* (Fig. 1B); and generally very low in the tribes that split off in the basal part of the phylogeny (Fig. 1A). Ryding (2007) suggested that the shared presence of large amounts of calyx fibers may indicate a relationship between the Lamioideae and Scutellarioideae. However, the present phylogeny (Fig. 1) suggests that high amounts of calyx fibers have evolved independently in these two subfamilies.

THE NEW CLASSIFICATION VERSUS HISTORICAL CLASSIFICATIONS

We are proposing a new suprageneric classification of subfamily Lamioideae with nine tribes (see Appendix 1). Three tribes are new and the remaining six tribes are recircumscribed to correspond to monophyletic groups in the current molecular phylogeny (Fig. 1). Several classifications of subfamily Lamioideae have been published in the past (e.g., Bentham, 1876; Briquet, 1895–1897). In the latest revision of the entire family (Harley et al., 2004), no suprageneric groups were recognized within subfamily Lamioideae. Neither of the historical classifications corresponds well to the current phylogeny, nor do they correspond well to the currently recognized subfamilies (sensu Harley et al., 2004). However, even if none of the groups in Bentham's (1876) and Briquet's (1895–1897) classifications represent monophyletic groups based on the current molecular phylogeny, a few remarks on how the new classification deviates from the historical ones are warranted.

There were no subfamilies in Bentham's classification; thus, most of the genera that are currently recognized as subfamily Lamioideae were placed in tribe Lamieae (as Stachydeae; Bentham, 1876; name corrected according to Sanders & Cantino, 1984). In addition to tribe Lamieae, Bentham also recognized tribe Prasieae, which included the fleshy-fruited genera

(Bentham, 1876). Also, the two lamioid genera *Pogostemon* and *Colebrookea* and the nepetoid genus *Tetradenia* Benth. were treated as subtribe Pogostemoninae (Pogostemoneae; name corrected according to Sanders & Cantino, 1984) under tribe Mentheae (as Satureineae; Bentham, 1876; name corrected according to Sanders & Cantino, 1984). Briquet's (1895–1897) classification was heavily influenced by Bentham's (1876) classification. The main difference between these two classifications was Briquet's recognition of a large subfamily Lamioideae (as Stachyoideae; name corrected according to Sanders & Cantino, 1984), which also included several taxa now known to belong in subfamily Nepetoideae (sensu Harley et al., 2004). Furthermore, subtribe Pogostemoninae was raised to the rank of tribe, i.e., as Pogostemoneae, and transferred to subfamily Lamioideae (sensu Briquet, 1895–1897) and Prasieae was raised to the rank of subfamily, i.e., as Prasioideae.

In both historical classifications, tribe Lamieae (sensu Bentham, 1876) and subfamily Lamioideae (sensu Briquet 1895–1897) were further divided into the three subtribes Melittidinae, Marrubiinae Endl., and Lamiinae Endl., the latter containing the vast majority of genera currently recognized as belonging to subfamily Lamioideae (Bentham, 1876; Briquet, 1895–1897). Thus, the most striking difference between the new classification proposed here (see Appendix 1) and these two historical classifications (Bentham, 1876; Briquet, 1895–1897) is that the genera they included in subtribe Lamiinae are split into several groups that are recognized at the tribal level.

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APPENDIX 1. A new tribal classification of subfamily Lamioideae includes nine tribes, three of which are new and five of which are circumscribed. Circumscription of tribe Synandreae follows a recently published study (Scheen et al., 2008). Asterisks (*) identify genera that are not included in the molecular analysis presented in Figure 1, but are still classified here according to other cladistic results or based on morphological similarities. All tribes represent monophyletic groups based on molecular data. To avoid phylogenetic redundancy, monogeneric tribes have not been accepted; hence, only clades that include more than one genus have been recognized and named as tribes. Consequently, a few genera that were included in the phylogeny and correspond to well-supported clades are still listed among genera incertae sedis. Non-molecular features that represent morphological characters shared by all or many of the members are given for all tribes. However, these morphological characters do not necessarily represent synapomorphies for the groups, but rather characters that are useful for identification.

1. Lamioideae Harley, *Kew Bull.* 58(3): 765. 2003. TYPE: *Lamium* L., *Sp. Pl.* 2: 579. 1753.

Non-molecular features: style gynobasic; nutlets not mucilaginous; pollen tricolpate and 2-celled when shed; seeds albuminous; embryo spatulate.

Included taxa: **Ajugoides* Makino, **Alajia* Ikonn., *Betonica* L., *Colquhounia* Wall., *Eriophyton* Benth., *Galeopsis* L., **Hypogomphia* Bunge, **Loxocalyx* Hemsl., **Matsumurella* Makino, **Metastachydium* Airy Shaw ex C. Y. Wu & H. W. Li, **Paralamium* Dunn, **Paraphlomis* (Prain) Prain, **Pseudomarrubium* Popov, *Roylea* Wall. ex Benth., **Stachyopsis* Popov & Vved., and **Sulaimania* Hedge & Rech. f., as well as Pogostemoneae, Gomphostemmatae, Synandreae, Stachydeae, Phlomideae, Leonureae, Lamieae, Marrubieae, and Leucadeae.

Note: *Ajugoides*, *Alajia*, *Hypogomphia*, *Loxocalyx*, *Matsumurella*, *Metastachydium*, *Paralamium*, *Pseudomarrubium*, *Stachyopsis*, and *Sulaimania* are included in subfamily Lamioideae based on the presence of tricolpate 2-celled pollen (Cantino & Sanders, 1986).

1. Pogostemoneae Briq. in Engl. & Prantl, *Nat. Pflanzenfam.* IV, 3a: 208. Dec. 1895. TYPE: *Pogostemon* Desf., *Mém. Mus. Hist. Nat.* 2: 154. 1815.

Non-molecular features: none readily apparent that could identify all or most members of this diverse clade. However, the following generally uncommon characteristics are comparatively frequent: bracts often very broad; corolla often weakly 2-lipped, posterior lip often short; stamens often

long-exserted, filaments often bearded; nutlets often small; pericarp often lacking a sclerenchyma region.

Included taxa: *Achyrosperrum* Blume, *Anisomeles* R. Br., **Colebrookea* Sm., *Comanthosphace* S. Moore, *Craniotome* Rehb., **Eurysolen* Prain, *Leucosceptrum* Sm., *Microtoena* Prain, *Pogostemon* Desf., *Rostrinucula* Kudô.

Note: *Colebrookea* is included in tribe Pogostemoneae based on morphological similarities: weakly 2-lipped corolla, short posterior lip; small nutlets. Also, *Eurysolen* is grouped with the other members of tribe Pogostemoneae in a molecular phylogeny based on the *trnL-F* region (results not shown).

2. Gomphostemmatae Scheen & Lindqvist, trib. nov.

TYPE: *Gomphostemma* Wall. ex Benth., Edwards's *Bot. Reg.* 15: t. 1292. 1830.

Inflorescentia saepe ex cyma laxa longipedunculata constans. Corolla plerumque grandis, tubo ad basim angusto distaliter valde dilatato, labio posteriore brevi vix cucullato. Nuculae carnosae vel siccae ac valde fibrosae.

Non-molecular features: inflorescences often lax, long-pedunculate cymes; corolla mostly large, with the tube narrow at the base but strongly dilated in the distal part; posterior lip short, scarcely hooded; nutlets fleshy or dry and strongly fibrous.

Included taxa: *Bostrychanthera* Benth., *Chelonopsis* Miq., *Gomphostemma* Wall. ex Benth.

3. Synandreae Raf., in *Fl. Tellur.* 3: 84, Nov.–Dec. 1837, as “Synandrinae.” TYPE: *Synandra* Nutt., *Gen. N. Amer. Pl.* [Nuttall] 2: 29. 1818.

Non-molecular features: inflorescence racemoid; flowers sessile or short-pedicellate; corolla tube broad; stamens villous.

Included taxa: *Brazoria* Engelm. & A. Gray, **Macbridea* Elliott ex Nutt., *Phylostegia* Benth., *Synandra* Nutt., *Warnockia* M. W. Turner.

Note: The inclusion of *Macbridea* is based on a previous molecular phylogeny (Scheen et al., 2008) and shared morphological characteristics: inflorescence racemoid; flowers sessile; corolla tube broad; stamens villous.

4. Stachydeae Dumort., *Fl. Belg.* (Dumortier) 44. 1827. TYPE: *Stachys* L., *Sp. Pl.* 2: 580. 1753.

Non-molecular features: none readily apparent that could identify all or most members of this diverse clade. However, the following characteristics are comparatively frequent: calyx often campanulate or weakly 2-lipped, calyx lobes often spiny, calyx throat often hairy; corolla often strongly 2-lipped.

Included taxa: *Chamaesphacos* Schrenk ex Fisch. & C. A. Mey., *Haplostachys* (A. Gray) Hillebr., *Melittis* L., *Phlomis* Vved., *Phyllostegia* Benth., *Prasium* L., *Sideritis* L., *Stachys* L., *Stenogyne* Benth. (nom. cons., non *Stenogyne* Cass. [Asteraceae]), *Suzukia* Kudô, *Thuspeinanta* T. Durand.

5. Phlomideae Mathiesen, trib. nov. TYPE: *Phlomis* L., *Sp. Pl.* 2: 584. 1753.

Trichomata ramosa ad plantae partes varias plerumque praesentia. Flos calycis lobis saepe in apicem angustum abrupte contractis, ad margines saepe expansis; corolla extus saepe barbata ac dense pubescente.

Non-molecular features: calyx lobes often abruptly narrowed to a narrow apex, often expanded at margins;

corolla often bearded and densely pubescent outside; branched hairs usually present.

Included taxa: *Eremostachys* Bunge, **Lamiophlomis* Kudô, *Notochaete* Benth., *Phlomis* L., *Phlomoideis* Moench, *Pseudereimostachys* Popov.

Note: *Lamiophlomis* is included based on morphological characteristics: calyx lobes abruptly narrowed to a spinescent apex, and corolla bearded and densely pubescent. Also, *Lamiophlomis* groups within *Phlomoideis* in a molecular phylogeny based on cpDNA data (Mathiesen et al., unpubl.).

6. Leonureae Dumort., Fl. Belg. (Dumortier) 46. 1827.
TYPE: *Leonurus* L., Sp. Pl. 2: 584. 1753.

Non-molecular features: $\pm$ palmate leaf venation; leaves often palmately lobed; stamens short.

Included taxa: *Chaiturus* Willd., *Lagochilus* Bunge ex Benth., *Leonurus* L., *Panzerina* Soják, **Lagopsis* (Bunge ex Benth.) Bunge.

Note: *Lagopsis* is included in tribe Leonureae based on morphological characteristics: palmately lobed leaves and short stamens. Also, *Lagopsis* grouped with the other members of tribe Leonureae in a molecular phylogeny based on *trnL-F* region (results not shown).

7. Lamieae Coss. & Germ., Fl. Descr. Anal. Paris 311, 324. 1845, as "Lamioideae." TYPE: *Lamium* L., Sp. Pl. 2: 579. 1753.

Non-molecular features: corolla often densely pubescent outside, posterior lip long, hooded, and often arched, tube usually abruptly widening; lateral lobes of the lower lip mostly with a tooth or acute at the apex; anthers mostly hairy.

Included taxa: *Lamium* L. (including *Lamiastrum* Heist. ex Fabr. and *Wiedemannia* Fisch. & C. A. Mey.).

8. Marrubieae Vis., Fl. Dalmat. 2: 214. 1847, as "Marrubiaceae." TYPE: *Marrubium* L., Sp. Pl. 2: 582. 1753.

Non-molecular features: calyx often with secondary lobes, often widely campanulate to rotate in the distal part.

Included taxa: *Ballota* L., *Marrubium* L., *Moluccella* L.

9. Leucadeae Scheen & Ryding, trib. nov. TYPE: *Leucas* R. Br., Prod. Fl. Nov. Holland. 504. 1810.

Flos calyce plerumque manifeste zygomorpha, lobis lobulatis; corollae labio superiore plerumque ad marginem barbato.

Non-molecular features: calyx usually distinctly zygomorphic with secondary lobes; upper lip of the corolla bearded at the margin, with few exceptions (*Acrotome* Benth. ex Endl.).

Included taxa: *Acrotome* Benth. ex Endl., *Isoleucas* O. Schwartz, *Leonotis* (Pers.) R. Br., *Leucas* R. Br., *Otostegia* Benth., *Rydingia* Scheen & V. A. Albert (Scheen & Albert, 2007).

GENERA INCERTAE SEDIS WITHIN LAMIOIDEAE

The six genera *Betonica*, *Colquhounia*, *Eriophyton*, *Galeopsis*, *Paraphlomis*, and *Roylea* have not been ascribed to any of the new or existing tribes at this point. *Betonica*, *Colquhounia*, *Galeopsis*, and *Paraphlomis* represent monogeneric clades in the current molecular phylogeny, thus ascribing them to monogeneric tribes would lead to phylogenetic redundancy. The relationships of *Eriophyton* and *Roylea* toward the remaining taxa are still uncertain because they are included either in a large polytomy (*Roylea*) or in a clade with poor support (*Eriophyton*). Some of the monotypic or small genera that for various reasons could not be included in the current survey of subfamily Lamiaceae are included in tribes due to strong morphological similarities to other genera in these groups. However, the following genera within the Lamiaceae are left unclassified at tribal level: *Ajugoides*, *Alajja*, *Hypogomphia*, *Loxocalyx*, *Matsumurella*, *Metastachydium*, *Paralamium*, *Pseudomarrubium*, *Stachyopsis*, and *Sulaimania*.

Note: An early draft of this paper was included in A.-C. Scheen's Ph.D. thesis (Scheen, 2007), which was printed in a very limited number and is not easily available to the public. In this early draft, we also included a tribe Betoniceae that included the resurrected genus *Betonica*. It was never our intention to let Scheen's Ph.D. thesis count as a proper publication neither of Betoniceae, nor of any other tribal names and recircumscriptions. We propose that the draft of the current new classification, as it was included in Scheen (2007), be disregarded as a proper publication.